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Los Angeles

A Multi-Modal Investigation
of Infant Visual Short-Term Memory

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Psychology

by

Andrew Jonathan Sanders

2021

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ABSTRACT OF THE DISSERTATION

A Multi-Modal Investigation of Infant Visual Short-Term Memory

by

Andrew Jonathan Sanders

Doctor of Philosophy in Psychology

University of California, Los Angeles, 2021

Professor Scott P. Johnson, Chair

The goal of this dissertation was to examine the scope and development of early visual short-term memory (VSTM) abilities in 6–12-month-old infants. *Study 1* investigated individual- and age-related differences across three unique VSTM tasks by examining the effect of increased delay on memory performance. Results suggest longer-term memory processes are quantifiable utilizing 500-1250 ms delays by 8 months with the Change Detection paradigm and spatial-attention cueing processes are quantifiable by 10 months with the Delayed Response paradigm. Performance improved from 6-12 months and longer delays impaired performance. *Study 2* examined whether fragile VSTM abilities were responsible for infants' A-Not-B error, a phenomenon often observed when searching for an object hidden at one of two locations (A and B). Six to 12-month-olds were assessed on a looking A-Not-B task as well as on Delayed Response and Change Detection to assess links between performance. Individual differences in VSTM performance were not predictive of A-Not-B error performance, providing evidence that VSTM

accounts may not solely provide explanation of A-Not-B error. *Study 3* assessed whether individual differences in 8-month-olds' neural band power was predictive of their VSTM performance. Infants' continuous EEG was recording during Change Detection as well as during a baseline resting-state. Results suggest the early alpha band modulates VSTM performance, with decreases in alpha band power shown for higher performers and increases in alpha band power shown for lower performers, relative to baseline. Theta band power was not found to be related to VSTM performance. These outcomes help inform the understanding of infant VSTM and its emergence throughout early development.

The dissertation of Andrew Jonathan Sanders is approved.

Catherine Sandhofer

Shafali Jeste

Craig Enders

Scott P. Johnson, Committee Chair

University of California, Los Angeles

2021

I would like to thank my parents, Shahla and David, for without them, none of this would be possible. Thank you for always believing in me and providing me with everything I have ever needed in life.

I would also like to thank my fiancé and future wife Stephanie, who was always there for me and gave me all the support and love that a partner can provide. I cannot wait to marry you and I look forward to all that life has in store for us!

My great appreciation goes to my mentor Dr. Scott Johnson for friendly collaboration throughout the years. His advice and guidance were highly valuable for the accomplishments of this dissertation and my development as a researcher.

I would also like to deeply thank Dr. Shafali Jeste for training me in electrophysiology prior to graduate school. Furthermore, I would also like to thank my statistics professors for providing me with a world-class education, specifically, Dr. Hongjing Liu, Dr. Jennifer Krull and Dr. Craig Enders. In addition, I would like to thank Dr. Catherine Sandhofer, Dr. Amber Ankowski and Dr. Iris Firstenberg for always believing in my teaching abilities.

I want to thank all families, babies, and research assistants who contributed to the studies at the UCLA Baby Lab. Without their reliable collaboration and commitment to our research projects, this dissertation would not have been possible.

Finally, I want to thank the University of California, Los Angeles, as I have belonged to this institution since I was an undergraduate. UCLA has always and will always continue to be a home to me. I will never forget the experiences I have made at this incredible university!

Go Bruins!

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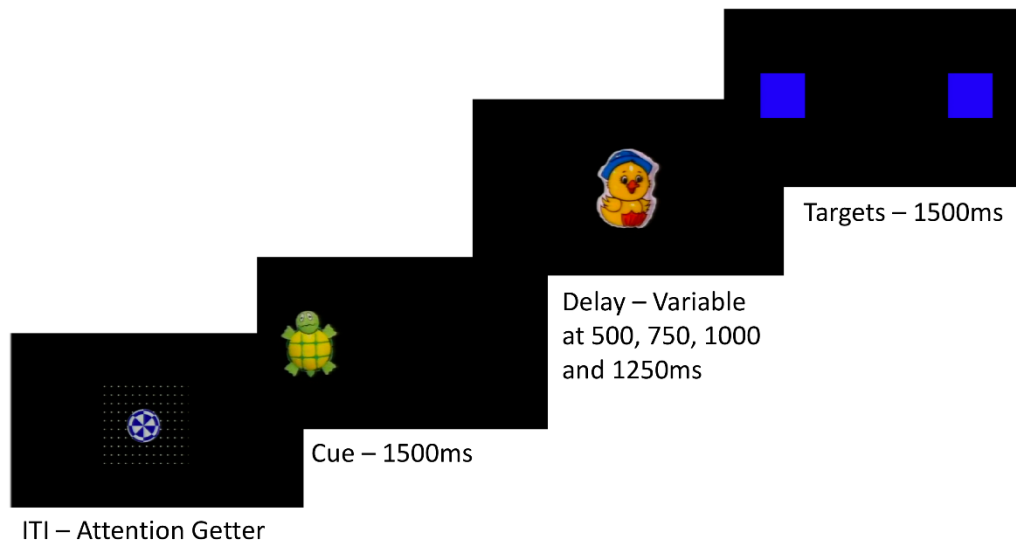


Figure 1. Delayed Response. Infants are presented with a centering stimulus, followed by a cue presented in a peripheral location (left or right) lasting for 1500 ms. Following the cue, a variable delay is imposed, consisting of delay periods of 500, 750, 1000, and 1250 ms. Following the delay, two identical targets are presented and remain on the screen for 1500 ms. Task success is determined by whether the infant first fixates on the AOI of the target appearing on the same peripheral side of the screen that the cue was previously shown.

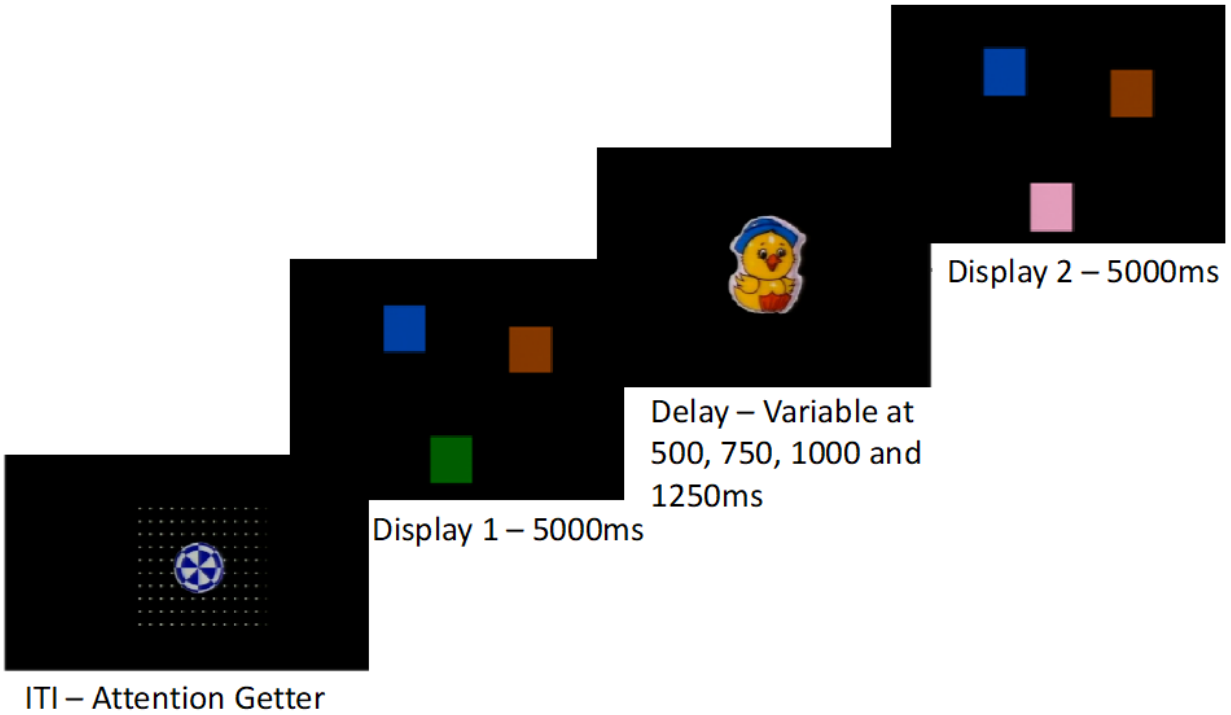


Figure 2. Change Detection. Infants are presented with a centering stimulus, followed by an array of three differently colored squares remaining on the screen for 5000 ms. Following the array, a variable delay is imposed consisting of delay periods of 500, 750, 1000, and 1250 ms. Following the delay period, the array of squares re-appears, except that one square’s color changed. Task success is determined by whether the infant first fixates on the AOI of the square that changed color.

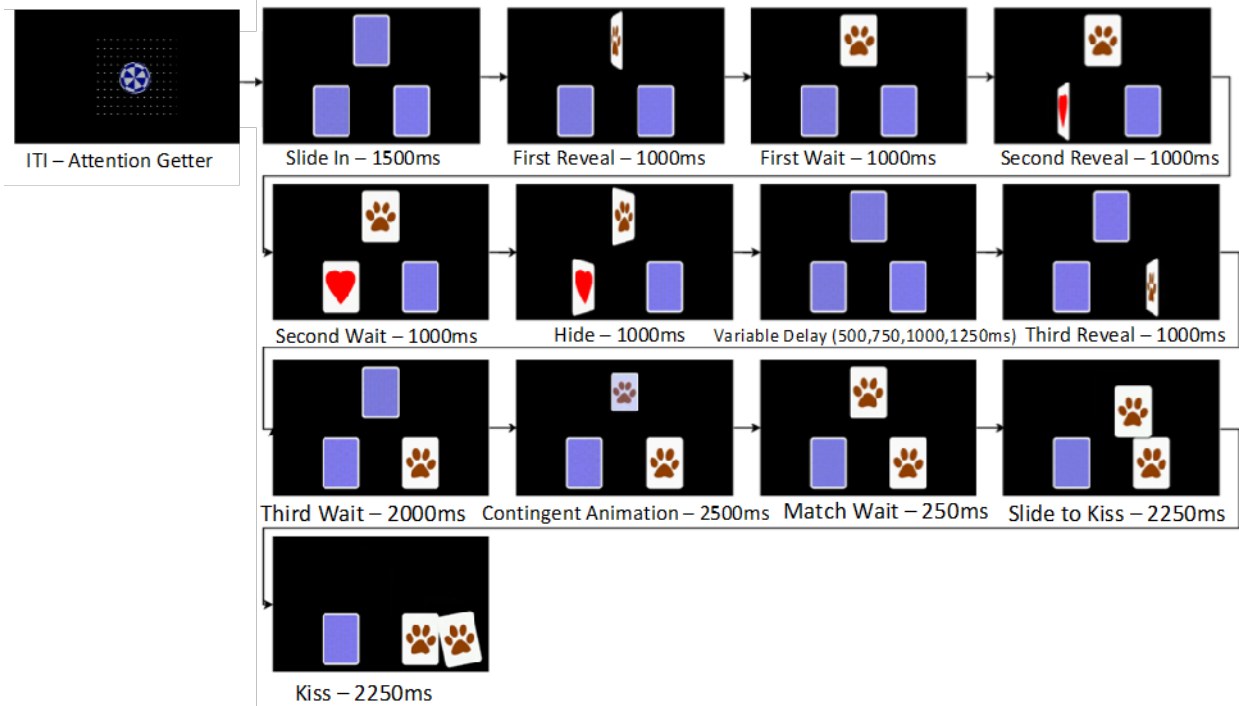


Figure 3. Delayed Match Retrieval. Infants are presented with a centering stimulus, followed by three face-down cards. One of the cards flips over to reveal its pattern and remains flipped-up while a second card on the screen also flips over to reveal its pattern. Following the flipping of these first two cards, the cards flip back downward, hiding the card’s pattern. While the cards remain face-down, a variable delay period was introduced consisting of delay durations of 500, 750, 1000, and 1250 ms. Following the delay period, the third card that was previously unexposed flips face-up to reveal its pattern and remains flipped up for 2000 ms. Task success is determined by whether the infant first fixates on the AOI of the face-down card that matches the pattern of the exposed card on the screen.

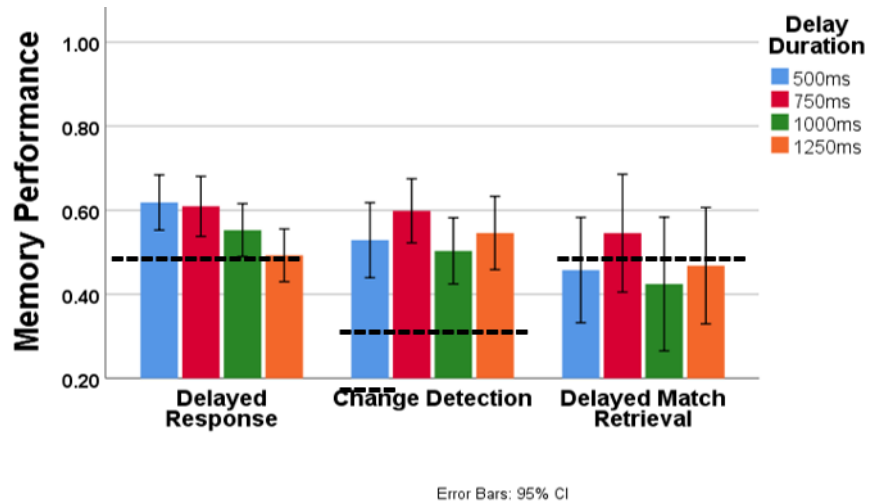


Figure 4. Average Memory Performance by Task and Delay Duration. Memory performance for Study 1 was computed for all infants and separated by task and delay duration. Infants performed significantly above chance levels (denoted by a dotted line) in Delayed Response (50%) and Change Detection (33.3%), but performance did not differ from chance in Delayed Match Retrieval (50%). Chance level performance is shown by the dotted black line. Error bars are displayed with 95% confidence intervals.

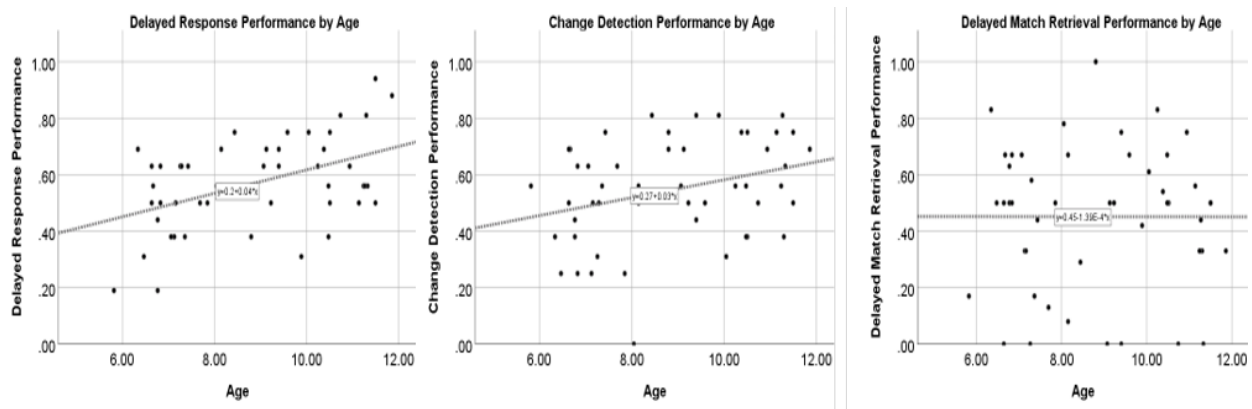


Figure 5. Developmental Trajectories in Memory Performance by Task. Developmental trajectories in Study 1 are plotted for individual tasks. Average performance for each task was collapsed across all delay durations and is plotted along the Y-axis, while age is plotted along the

X-axis. The resulting R^2 linear values are given for the following tasks: Delayed Response ($R^2=0.213$), Change Detection ($R^2=0.095$), and Delayed Match Retrieval ($R^2<0.001$). For Delayed Response, results suggest linear increases in average memory performance from above 40% at 6 months to above 60% at 12 months. For Change Detection, average memory performance also increased linearly from above 40% at 6 months to above 60% at 12 months. For Delayed Match Retrieval, average memory performance showed no age-related increases.

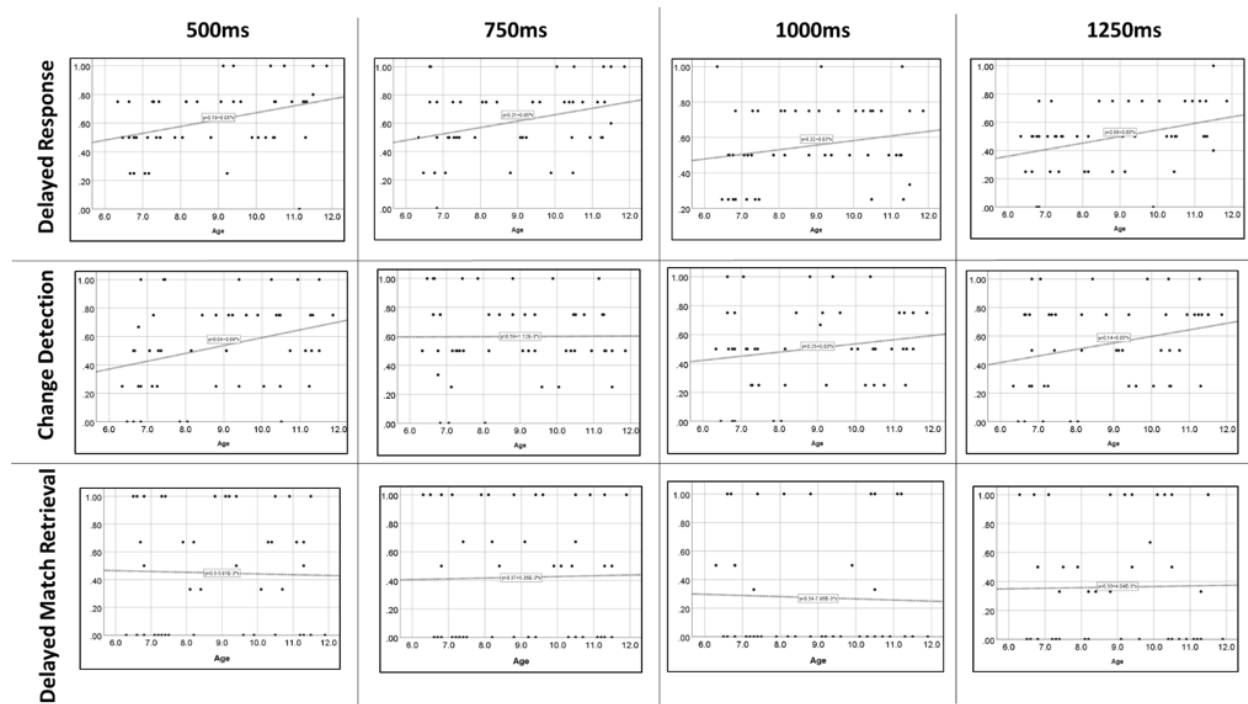


Figure 6. Developmental Trajectories in Performance by Task and Delay. Developmental trajectories in Study 1 are plotted by each delay period for individual tasks. Average performance for each task is plotted along the Y-axis, while age is plotted along the X-axis. The resulting R^2 linear values are given for the following tasks and delays: Delayed Response (500 ms: $R^2=0.135$, 750 ms: $R^2=0.102$, 1000 ms: $R^2=0.043$, 1250 ms: $R^2=0.139$), Change Detection (500 ms: $R^2=0.097$, 750 ms: $R^2<0.001$, 1000 ms: $R^2=0.033$, 1250 ms: $R^2=0.070$), and Delayed Match Retrieval (500

ms: $R^2 < 0.001$, 750 ms: $R^2 < 0.001$, 1000 ms: $R^2 = 0.001$, 1250 ms: $R^2 < 0.001$). For Delayed Response, results suggest age-related increases in average performance from 6 to 12 months across all delay durations. For Change Detection, average performance also increased linearly across age for all delays except for 750 ms. For Delayed Match Retrieval, average performance showed no age-related increases across any delays.

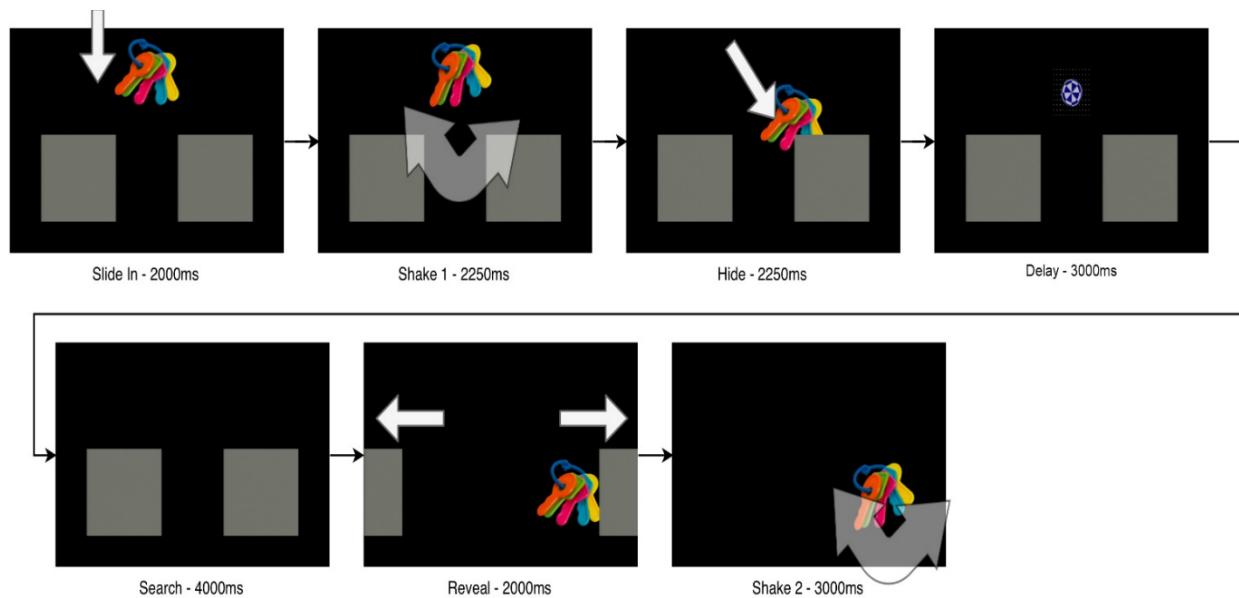


Figure 7. Oculomotor A-Not-B. Infants in Study 2 were presented with a set of keys in a central location at the top of the screen. The keys then shook back and forth, and then moved into one of two hiding locations. For the first and second trials, the keys were always hidden in the same location. However, during the third trial, the keys were instead hidden in the other hiding location. The delay period was 3000 ms.

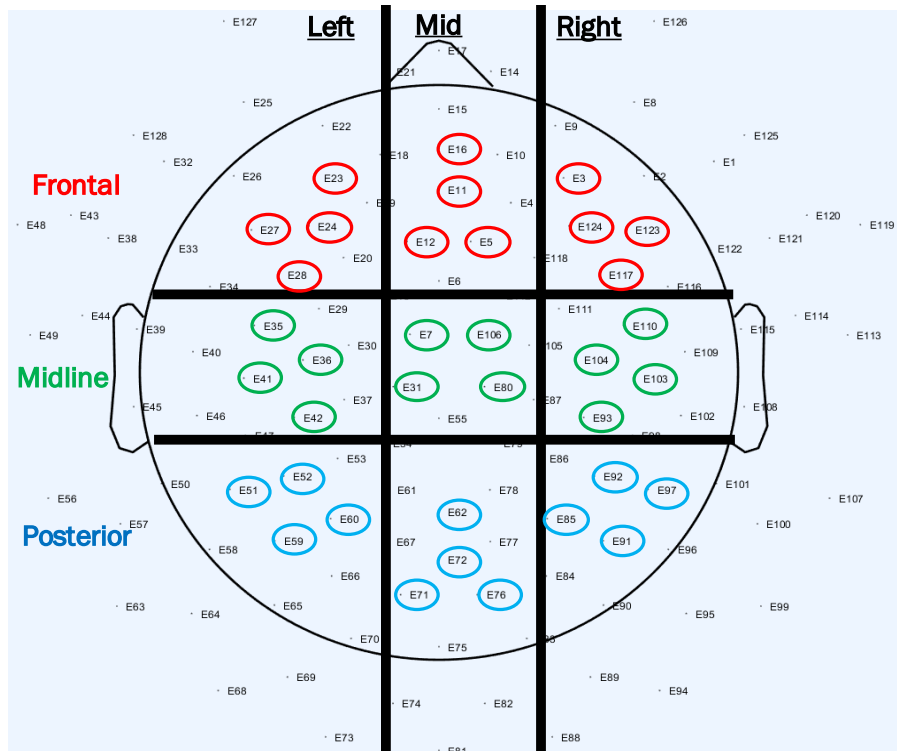


Figure 8. Electrode Locations. Neural regions of interest were chosen for three different brain regions: frontal, midline, and posterior. Furthermore, each brain region was further broken down into 3 sub-regions: left, mid, and right. This resulted in 9 different possible neural areas of interest: left-frontal, mid-frontal, right-frontal; left-midline, mid-midline, right-midline; left-posterior, mid-posterior, right-posterior.

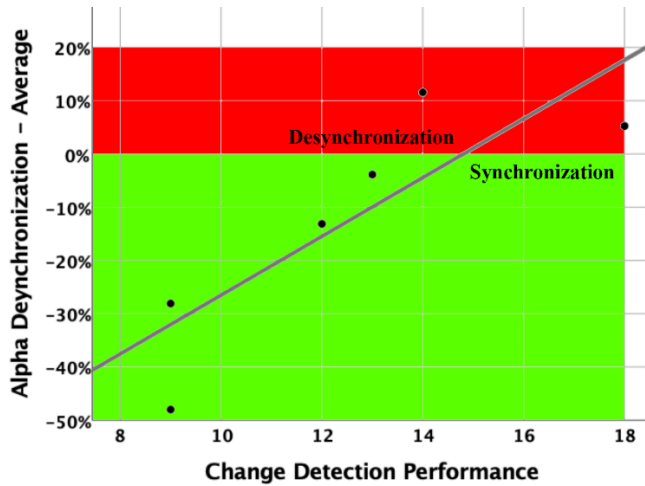


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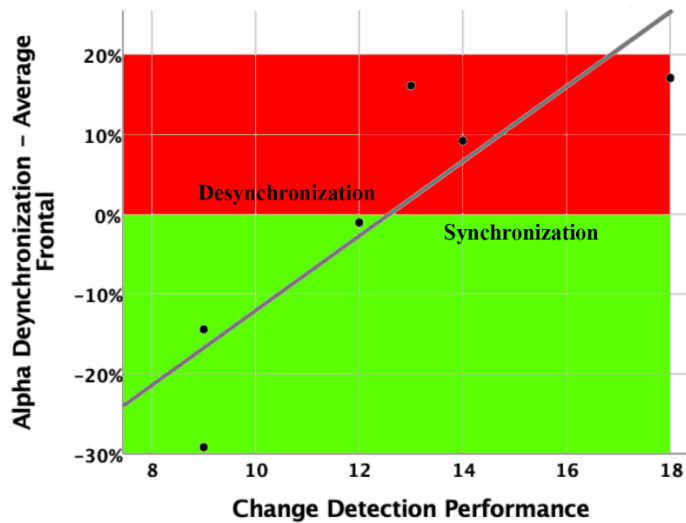


Figure 10. Frontal Alpha Desynchronization. Correlations are shown between average Change Detection performance (out of 24 possible trials) and average alpha desynchronization in the brain's frontal region ($R^2=0.742, p=0.028$).

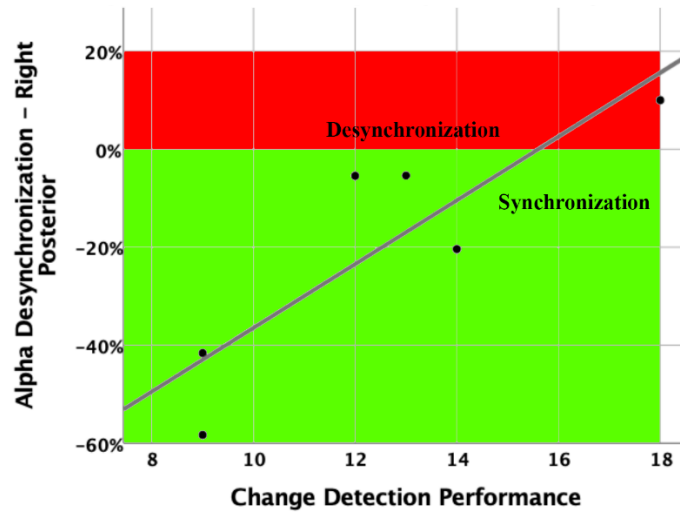


Figure 11. Right-Posterior Alpha Desynchronization. Correlations are shown between average Change Detection performance (out of 24 possible trials) and average alpha desynchronization in the right-posterior region of the brain ($R^2=0.747$, $p=0.026$).

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| Model Term | Coefficient | Exp(Coefficient) | Std. Error | t | Sig. |
|--------------------------------|----------------|------------------|------------|--------|---------|
| Intercept | -1.583 | 0.205 | 1.253 | -1.264 | 0.207 |
| Delayed Response | 0.483 | 1.621 | 0.146 | 3.320 | 0.001* |
| Change Detection | 0.390 | 1.477 | 0.155 | 2.521 | 0.012* |
| Delayed Match Retrieval | 0 ^a | Task Reference | | | |
| 500 ms Delay | 0.243 | 1.258 | 0.133 | 1.828 | 0.068 |
| 750 ms Delay | 0.388 | 1.474 | 0.136 | 2.851 | 0.005* |
| 1000 ms Delay | 0.060 | 1.062 | 0.132 | 0.458 | 0.647 |
| 1250 ms Delay | 0 ^a | Delay Reference | | | |
| Age | 0.136 | 1.145 | 0.028 | 4.775 | <0.001* |

Table 1. GLMM Fixed Coefficients. The fixed coefficients output from the GLMM in Study 1 utilized task type, delay duration, and age. The reference variables for the analysis include Delayed Match Retrieval (Task reference) and 1250 ms (Delay reference). Log odds are noted in the column labeled “Coefficient.” Odds ratios are noted in the column labeled “Exp(Coefficient).” The intercept term is included, but should not be meaningfully interpreted.

| | Left | Mid | Right |
|------------------|----------------|----------------|-------------------|
| Frontal | 3, 24, 27, 28 | 5, 11, 12, 16 | 3, 117, 123, 124 |
| Midline | 35, 36, 41, 42 | 7, 31, 80, 106 | 93, 103, 104, 110 |
| Posterior | 51, 52, 59, 60 | 62, 71, 72, 76 | 85, 91, 92, 97 |

Table 2. EEG Electrode locations. Electrode locations for Study 3 were chosen based on areas of interest on the scalp. Specifically, regions included: left-frontal, mid-frontal, right-frontal, left-midline, mid-midline, right-midline, left-posterior, mid-posterior, right-posterior.

| | Frontal | Midline | Posterior |
|------------------------------|----------------|----------------|------------------|
| Theta (Resting-state) | 55.394 | 48.983 | 79.625 |
| Theta (Task-state) | 60.767 | 56.885 | 98.763 |
| | | | |
| Alpha (Resting-state) | 11.142 | 11.355 | 18.886 |
| Alpha (Task-state) | 11.364 | 13.241 | 23.369 |

Table 3. Mean Power Values by Region. Mean power values for Study 3 are shown for the theta and alpha rhythm at both resting-state and task-state for frontal, midline, and posterior neural regions of interest.

| | Left-Frontal | Mid-Frontal | Right-Frontal | Left-Midline | Mid-Midline | Right-Midline | Left-Posterior | Mid-Posterior | Right-Posterior |
|------------------------------|---------------------|--------------------|----------------------|---------------------|--------------------|----------------------|-----------------------|----------------------|------------------------|
| Theta (Resting-state) | 54.424 | 56.892 | 54.867 | 46.319 | 42.360 | 40.970 | 94.516 | 85.024 | 59.333 |
| Theta (Task-state) | 59.110 | 61.670 | 61.520 | 65.407 | 57.515 | 65.035 | 109.100 | 111.421 | 75.768 |
| | | | | | | | | | |
| Alpha (Resting-state) | 12.182 | 10.793 | 10.450 | 13.017 | 13.373 | 12.207 | 20.375 | 21.794 | 14.488 |
| Alpha (Task-state) | 12.334 | 10.788 | 10.970 | 14.003 | 8.690 | 12.496 | 25.664 | 27.346 | 17.096 |

Table 4. Mean Power Values by Sub-Region. Mean power values for Study 3 are shown for the theta and alpha rhythm at both resting-state and task-state for: frontal, midline, and posterior neural regions of interest separated by: left, mid, and right sub-regions.

Acknowledgements

Study 1 is a version of “Indexing visual memory durability in infancy”

Sanders, A. J., & Johnson, S. P. (2021). Indexing Early Visual Memory Durability in Infancy. *Child Development, 92*(2), e221-e235.

Study 2 is a version of “Testing a memory account of A-Not-B error”

Sanders, A. J., & Johnson, S. P. (2021). Testing a memory account of the A-not-B error. *Infant Behavior and Development, Under Review*.

Vita / Biographical Sketch

The author, Andrew Sanders, received his education at the University of California, Los Angeles. He has previously obtained an M.A. and B.A. in psychology. He received multiple awards during his time at UCLA, including: *UCLA Shepard Ivory Franz Psychology Teaching Assistant Award* (2020), *UCLA Dean's Excellence Award* (2020), *UCLA Summer Teaching Practicum Program* (2020), *UCLA Department Graduate Summer Research Fellowship* (2019), *Cognitive Development Society Diversity Travel Award* (2017), *UCLA Graduate Summer Research Mentorship Fellowship* (2017, 2016). He has published works including: Sanders, A. J. & Johnson, S. P. (2021). *Indexing early visual memory durability in infancy*. *Child Development* ; Sanders, A. J. & Johnson, S. P. (2021, Under Review) *Testing a memory account of A-Not-B error*. *Infant Behavior and Development* ; Felt, L., Sanders, A. J. & Uhls, Y. T. (2021, In Press) *Investigating Viewership of Season 3 of 13 Reasons Why and the Mental Wellness of Adolescents: Partially Randomized Preference Trial*. *JMIR Mental Health* ; Jeste, S. S., Kirkham, N., Senturk, D., Hasenstab, K., Sugar, C., Kupelian, C., Baker, E., Sanders, A. J., Shimizu, C., Norona, A., Paparella, T., Freeman, S., & Johnson, S. P. (2014). *Electrophysiological evidence of heterogeneity in visual statistical learning in young children with ASD*. *Developmental Science*, 18(1), 90-105 ; McEvoy, K., Hasenstab, K., Senturk, D., Sanders, A. J., & Jeste, S. S. (2015). *Physiologic artifacts in resting state oscillations in young children: Methodological considerations for noisy data*. *Brain Imaging and Behavior*, 9(1), 104-114.

General Introduction

Visual short-term memory (VSTM) is a fundamental cognitive process utilized across the human lifespan on a moment-by-moment basis. Defined as a limited-capacity cognitive system used to temporarily store small amounts of visual information for short periods of time, it is known to be available to infants by 4 months of age (Reznick et al., 2004; Ross-Sheehy et al., 2003). Fundamental components of executive functions, such as VSTM, begin to develop and mature throughout infancy and childhood and into adolescence, forming a critical foundation that sets the stage for development of higher-order cognitive processes such as planning, reasoning, and problem solving (Collins & Koechlin, 2012). The development of these processes plays an important role across a variety of domains during childhood, including emotion regulation (Eisenberg et al., 2007), school readiness (Blair & Razza, 2007), and social cognition (Blakemore & Choudhury, 2006).

Developmental theorists have long suggested that individual variability in cognitive abilities such as VSTM may underlie individual differences in fluid intelligence, a domain-general mechanism thought to underlie reasoning, problem solving, and analysis of novelty (Colom et al., 2008; Conway et al., 2003; de Abreu et al., 2010; Deary et al., 2007; McCall & Carriger, 1993; Sedek et al., 2016). Assessments of infant VSTM have shown to be predictive of memory abilities in later childhood, suggesting that memory remains relatively stable throughout development. A longitudinal study assessed infants at 7-, 12-, 24-, and 36-months-old via habituation and imitation tasks and tested those same individuals on working memory abilities at 11-years-old. Results showed that lower performing individuals at an early age continued to struggle with working memory performance later on (Rose et al., 2003). In addition, early measures of memory have been shown to be predictive of academic performance in later childhood. A longitudinal study

investigated the relation between both early memory skills and IQ at 5 years and later academic success at 11 years, and found that early memory skills better predicted later math and reading skills than did IQ (Alloway & Alloway, 2010). The authors concluded that early memory skills may not only predict later IQ, but may also uniquely predict academic achievement over and above IQ scores.

These aforementioned studies indicate that infant memory abilities may predict later performance on measures of memory and intelligence, yet developmental growth in infant VSTM is poorly understood, especially compared to the wide body of literature available from older children and adults. Thus, the goal of the current dissertation was to closely investigate infant VSTM abilities in the first post-natal year in order to examine its development and emergence on a behavioral and neurological level. The motivation for the set of studies presented in this dissertation is outlined below.

VSTM Capacity and Durability

Shorter-term memory processes are often operationalized in terms of capacity, such as the maximum number of discrete objects / objects features that can be successfully maintained over a certain duration of time (Oberauer & Kliegl, 2006), and can also be measured in regards to durability. Memory durability is defined as the maximum length of time that information can be successfully retained (Pelphrey & Reznick, 2003; Reznick, 2008). When information must be maintained over longer delay durations there is a demand increase placed on memory systems regardless of the number of discrete stimuli to be remembered. For example, adult studies have shown that increasing levels of cognitive demand via increased temporal delay can significantly restrict memory abilities (Barrouillet & Camos, 2012). These constraints are modulated in part by cognitive load, defined as the combined cognitive effort required for success during memory tasks

(Sweller, 1988). That is, when there is the requirement to maintain information with an increasing delay period, there is an inherent increase in demand on memory systems.

Tasks designed to measure VSTM abilities typically comprise three key phases, each focusing on different memory sub-mechanisms (Oberauer et al., 2003):

1. *Encoding*. The transformation of information leading to the creation of new content. In other words, information must first be encoded before it is stored as a memory representation. Cognitive load can be manipulated during this task-phase by varying the amount of information required to be encoded.
2. *Maintenance*. The preservation of new information over a brief period. Over the course of a delay, temporarily stored memory representations are susceptible to decay. Interference can also be introduced during the delay to exacerbate the rate of decay of memory traces during maintenance. Cognitive load can be manipulated during this task-phase by varying the time that infants must retain information in memory.
3. *Retrieval*. The monitoring and control of current cognitive operations using selective attention of relevant content and the inhibition of irrelevant content. An example of retrieval is choosing the correct location of an occluded object after a delay. Cognitive load can be manipulated during this task-phase by varying the number of distractor stimuli included alongside the target stimulus.

Due to obvious constraints of testing infants, developmental researchers are often times limited in objective ways to test infant memory abilities. However, a body of literature described next provides evidence that early VSTM can be indexed via different tasks using brief delay periods.

Infant Memory Assessments

Delayed Response. Delayed Response is a procedure used to assess frontal lobe function (Hunter, 1913). Participants are cued briefly with an auditory or visual stimulus until it is withdrawn, and after a short delay period, they attempt to identify the location where the stimulus appeared. In one popular developmental adaptation of the paradigm, infants are seated on a caregiver's lap, facing directly opposite an experimenter. In between the infant and experimenter is a table containing two hiding wells, and small cloths used to cover the hiding wells. A toy is first hidden in one of the two wells, and the infant is allowed to reach to the well to find the toy (Diamond & Doar, 1989). The task is similar to the Piagetian A-Not-B task, but differs because the side of hiding is varied randomly over trials, while in the A-Not-B task the toy is repeatedly hidden in the same well until the infant makes a correct reach, and then the side of hiding reverses (Piaget, 1955). Delayed Response has also been adapted to use oculomotor behavior as the dependent measure (Funahashi et al., 1989). Instead of coding reaching behaviors, oculomotor paradigms code the trial as a pass if the infant's first fixation or looking time is directed to the same target location as the previous cue stimulus.

Because the location of the cue stimulus randomly changes on a trial-by-trial basis, Delayed Response success requires maintaining representations of a previously cued visual stimulus over short delays. Studies utilizing Delayed Response procedures have found visual memory durability at 6 months of 1-2 s (Reznick et al., 2004) and 3-5 s delays (Gilmore & Johnson, 1995), with performance increasing to 10–20 s by 9 months (Schwartz & Reznick, 1999). Furthermore, memory durability was reported to undergo significant developmental improvement, linearly increasing by approximately 2 s each month of development from delays of 2 s at 7.5 months to 12 s at 12 months (Pelphrey et al., 2004). Another developmental study of Delayed

Response reported success at 250 ms delays by 8 months, with performance improving to success at 9 s by 12 months (Brody, 1981).

Change Detection. The Change Detection visual memory task requires infants to assess changes across multiple-item arrays over a short delay. In a typical trial, infants are presented with a set of objects appearing in discrete positions on the screen that each contain a given number of specific stimulus features (e.g., size, color). Following initial array presentation, a delay is imposed in which the infant is meant to maintain information in memory. After the delay, the array reappears, with one stimulus having changed features (e.g., color). During this phase, oculomotor fixations and looking times are recorded. If the infant's first fixation or total looking time is directed to the changed target stimulus, the trial is coded as a pass.

Studies using the Change Detection task in infancy have also reported notable developmental performance improvements. In one study, for example, 6- and 8-month-olds were shown a pair of 2 object arrays with a delay of 317 ms between arrays, 8-month-olds exhibited a preference for an item that changed color, evidence that memory for that item persisted across the delay. Six-month-olds exhibited no evidence for object memory under these conditions, but when the initial pair of squares was identical, they showed preference for the changed item, indicating successful memory (Oakes et al., 2013).

The Change Preference task was developed for younger infants and is thought to tap the same construct as the Change Detection task. In the Change Preference task infants view two separate screens in alternation, one displaying constant stimulus arrays and the other displaying arrays with a color change. Set size is manipulated by varying the number of stimuli in each array. Six-month-olds were found to look significantly longer to changing streams of 1 object, and 10- to 13-month-olds looked significantly longer to changing streams with displays of up to 4 objects

(Ross-Sheehy et al., 2003). A second Change Preference study found that 6.5-month-olds did not perform successfully on 3-item arrays with 300 ms delays, but 7.5- and 12.5-month-olds were successful, with no improvement after 7.5 months. These results were attributed to development of an ability to bind features and store multiple objects between 6.5-7.5 months, a process mediated by the posterior parietal cortex and likely related to focused attention (Oakes et al., 2013; Oakes et al., 2006).

Delayed Match Retrieval. The Delayed Match Retrieval task is an oculomotor-adapted delayed match-to-sample paradigm that assesses visual memory for object-location bindings by utilizing anticipatory gaze responses as the dependent measure (Kaldy et al., 2016). Infants are initially presented with an array of three face-down virtual playing cards. Two cards are sequentially revealed, followed by a delay during which all cards are again face down, and then revealing of the third card. If infants look immediately to the corresponding face-down card that matches the remaining face-up card, the trial is coded as a pass. Kaldy et al. found that 10-month-olds, but not 8-month-olds, performed significantly above chance levels for delays of 1.5 s, indicating successful memory for object-location information.

Taken together, these findings demonstrate that early VSTM processes can be indexed by 6 months, as measured by a variety of unique tasks, and that performance improves with age. Notably, however, estimates of early VSTM durability are highly variable across different tasks for same-aged infants. For example, estimates of VSTM durability in 8-month-olds in Delayed Response studies ranged from 250 ms (Brody, 1981) to 2 s (Pelphrey et al., 2004). Furthermore, results across studies suggest infants are able to perform successfully at longer delays in Delayed Response tasks vs. Change Detection and Delayed Match Retrieval tasks, presumably due to differences in task demands. For example, 12-month-olds showed evidence for retaining spatial

information for a single object at delays up to 12 s in a Delayed Response task (Pelphrey et al., 2004), but in a Change Preference task, 12.5-month-olds failed to discriminate arrays of set size three for delays around 300 ms (Oakes et al., 2013). In a Delayed Match Retrieval task, 10.5-month-olds retained location information for two distinct stimuli in memory for only 1.5 s (Kaldy et al., 2016). These discrepancies necessitate the need for a more stringent examination of infant VSTM utilizing the aforementioned tasks.

A-Not-B Task.

Piaget's classic A-Not-B task provides a measure of an infant's search for a hidden object. The task requires infants to search for an object hidden in one of two locations (Location A and Location B), often with a delay imposed between hiding and searching so that memory is required to locate the object. In a typical trial, the experimenter introduces an object to be hidden to the infant. The experimenter then hides the object in one of the two locations, with or without a delay, and breaks the infant's gaze to the locations. The infant is then allowed to search for the object. If the infant reaches to the correct hiding location it is assumed they have successfully maintained the memory trace of the hidden object's location prior to search.

The so-called "A-Not-B error" occurs when infants continue searching at the incorrect location ("Location A") instead of the correct location ("Location B") after several successful reaches at the prior location. This happens when the experimenter switches hiding locations from the original Location A (where the infant previously searched successfully) to the new Location B. Infants younger than 10 months often fail to search for the object at Location B and continue perseverative searching at Location A despite directly observing the object being hidden at Location B, even with no delays introduced between hiding and searching (Piaget, 1955).

VSTM abilities are available to infants by 4 months of age as shown with successful

performance across a wide variety of tasks (Reznick et al., 2004; Ross-Sheehy et al., 2003), yet infants up to 12 months still struggle to succeed on the A-Not-B task (Piaget, 1955). The A-Not-B task has been thought of as a developmental milestone and has been used as an early marker of infant memory abilities (Cummings & Bjork, 1983a, 1983b), since successful performance has been found to be a function of delay between hiding, search, and age (Diamond, 2013). Furthermore, A-Not-B performance in 10-12-month-olds may be linked to the onset of later executive functions in early childhood, predicting future abilities such as inhibition, working memory, and cognitive flexibility (Diamond, 2013).

Piaget originally attributed the A-Not-B error as the infant's understanding of an "object concept," defined as a continuing understanding that objects' spatial and temporal properties persist after they are no longer visible. However, work following Piaget sought to explain the A-Not-B error in a number of different ways. From a cognitive perspective, the A-Not-B error has been thought to reflect the functioning of early executive functions that develop during infancy, including attention, inhibition, memory, and task switching (Diamond et al., 1997; Funahashi et al., 1993; Goldman-Rakic, 1987; Nelson, 1995). Furthermore, A-Not-B errors have been shown to increase with the use of longer delay durations (Diamond, 1990b), suggesting that VSTM abilities may indeed play a role in the error. From a neuroscience perspective, an electrophysiological study of infant brain activity during tasks similar to A-Not-B revealed the 6-9 Hz frequency band (the alpha band, believed to be a neural correlate of infants' cognitive abilities) was informative in differentiating correct and incorrect responses (Bell, 2002). These cognitive and neuroscience perspectives have provided evidence to a memory account of the infant A-Not-B error.

However, there is also evidence suggesting A-Not-B error performance does not provide

an accurate measure of infant memory abilities. Due to the motor requirements inherent in the reaching-based task, consecutive hiding trials at Location A have been thought to produce a prepotent motor reaching response to Location A, independent of memory, that is difficult for younger infants to overcome when subsequently switching to search at Location B (Smith et al., 1999). Specifically, perseverative reaches back to Location A could be “the product of the processes that take a hand to a location in visual space: the body-centered nature of the spatial code, memories for previous reaching activity, and the close coupling of looking and reaching (p. 235).” Furthermore, A-Not-B error rate is known to decrease considerably for 10-month-olds by simply withholding typical communicative cues used by experimenters. Authors explain that cues typically used mislead infants in the context of the hiding-based game, and by excluding this aspect altogether, infants are less likely to perseverate back to Location A (Topál et al., 2008). A U-shaped developmental pattern of performance has also been reported: Infants were found to search correctly in the A-Not-B task without hidden items at 5 months, but the same infants later went on to make the A-Not-B error at 7- and 8 months, with performance again improving closer to 12 months (Clearfield et al., 2006). In addition, a meta-analysis concluded that age, number of prior Location A hiding trials, number of total hiding locations, distances between hiding locations, and the array’s distinctive visual properties all influence infants’ A-Not-B performance (Marcovitch & Zelazo, 1999; Marcovitch et al., 2002). Performance on the A-Not-B task has also been found to be highly variable at numerous ages tested, such that for same-age infants there was a mix of above-chance and below-chance performance found (Bremner, 1978; Bremner & Bryant, 1977).

The aforementioned body of literature suggests that VSTM abilities alone may not play a role in infants’ reaching A-Not-B Error performance. Thus, studies sought to move away from the extra demands inherent in the reaching A-Not-B task and instead assess infants’ looking responses.

In one such study, researchers found no differences in A-Not-B performance assessed via looking and reaching versions for 8-month-olds (Bell & Adams, 1999). However, a similar study showed that 8-12-month-olds who failed the reaching version were capable of passing a looking version—that is, infants looked toward the correct hiding location (Ahmed & Ruffman, 1998), implying that oculomotor responses may provide a reliable index of A-Not-B performance. These aforementioned discrepancies, when taken together, necessitate the need for a more stringent examination of what underlies the infant A-Not-B error.

Neural Correlates of VSTM Performance

Infant research using electroencephalogram (EEG) techniques has increased in recent years due to interest in understanding the neural processes involved in early cognitive development. EEG allows for a direct measure of scalp-level neural activity with high temporal precision and is useful for non-verbal populations like infants. Cognitive processes like memory arise from functionally organized brain processes mediated by large-scale synchronous neuronal activity (Anderson & Bower, 1974). Researchers utilize EEG to identify brain processes closely associated with cognitive processes like memory and how the former gives rise to the latter. Quantitative EEG (qEEG) analysis allows for the decomposition of a continuous EEG signal, using a Fast Fourier Transform (FFT) (Brigham, 1988), into underlying frequency bands that each exhibit certain functional characteristics. In particular, frequency bands such as alpha and theta have shown promise as neural markers of cognitive performance, with both rhythms thought to underly inhibitory control abilities that support VSTM performance. Much work in the adult and older childhood cognitive literature has identified alpha and theta oscillations as neural correlates of successful memory performance, as outlined below.

Alpha Band. Alpha oscillations are thought to reflect top-down inhibition of non-essential visual processes that support memory (Klimesch, 1997; Lebedev, 1994), arising from thalamo-cortical feedback loops in the brain (Klimesch et al., 1994; Steriade et al., 1990). Specifically, alpha is thought to be involved when searching for or identifying previously encoded information (Klimesch, 1996); as alpha oscillations increase, the brain has faster access to previously encoded information. As noted previously, the alpha band is characterized as the 6-9 Hz range in infants and can be observed by 3 months (Stroganova et al., 1999). *Alpha desynchronization* is defined as an attenuation of alpha rhythms during task-state cognitive mental activity, leading to an amplitude decrease relative to a baseline resting-state. During memory tasks, higher levels of alpha desynchronization are associated with better memory performance. Adult studies have shown less pronounced alpha desynchronization for lower performers during memory tasks, perhaps because higher performers increase their attention after a memory set is presented, while lower performers' substandard attentional ability (marked by lower levels of alpha desynchronization) hinders performance (Klimesch et al., 1993). Evidence from adults further suggests that alpha desynchronization increases linearly as a function of increasing level of cognitive load, as shown when manipulating set size on a forward span task (Stipacek et al., 2003). Infant studies have shown that alpha desynchronization is related to attentional processes during cognitive tasks, such as sustained attention (Xie et al., 2018) and basic visual attention to a stimulus (Orekhova et al., 1999). Additionally, alpha desynchronization was shown to discriminate between infants' correct and incorrect responses on a cognitive task (Bell, 2002; Bell & Wolfe, 2007). Higher levels of alpha desynchronization have also been reported when infants process novel numbers, as opposed to familiar numbers (Libertus et al., 2009). Authors explained that the greater amount of allocated attention needed for the processing of novel numbers drove greater alpha desynchronization.

Theta Band. Theta oscillations are thought to determine the speed and precision of memory, arising from underlying hippocampal neural activity related to executive control of attention (Burgess & Gruzelier, 1997). The infant theta band is characterized as the 2-6 Hz frequency range (Orekhova et al., 2006) and it can be observed by 3 months (Stroganova et al., 1999). *Theta synchronization* is defined as a strengthening of theta power during task-state cognitive mental activity, leading to an amplitude increase relative to baseline resting-state. Studies with adults and older children have shown that increases in theta power during cognitive assessments are associated with higher performance, especially on tasks requiring memory (Gevins et al., 1997; Kahana et al., 2001; Khader et al., 2010; Sauseng et al., 2010; Werkle-Bergner et al., 2006). Furthermore, cognitive load as manipulated via increased task demands correlates with increased theta synchronization (Krause et al., 2000). Studies with infants have also demonstrated increases in theta synchronization during periods of internally controlled attention (Orekhova et al., 1999). Theta synchronization is also related to sustained attention (Xie et al., 2018) and anticipatory looking behaviors (Orekhova et al., 1999).

High vs. Low Performers. Studies from the adult and older childhood literature have explored the relationship between alpha and theta power and cognitive performance, with results demonstrating that power decreases in the alpha band (alpha desynchronization) and power increases in the theta band (theta synchronization) are both associated with better memory performance (Werkle-Bergner et al., 2006). Both bands are promising markers of VSTM performance, with higher performers displaying both lower levels of alpha power and higher levels of theta power during cognitive tasks, and lower performers displaying higher levels of alpha power and lower levels of theta power. However, this relationship between alpha, theta, and memory performance still remains largely unexplored in infancy.

Specific Aims

Understanding the development of human cognition by systematically investigating the conditions under which early memory operates, including - (i) the scope and limits of its capacity and durability, (ii) its relation to important developmental milestones, and (iii) its relation to underlying brain activity - will each be important for recognizing how early memory comes to affect general and complex cognitive functions in later life. Taken together, aforementioned discrepancies among previous findings and a lack of direct investigation necessitate the need for a stringent examination of infant VSTM abilities using multiple methodologies and modalities to address the following specific aims:

Study 1: *Indexing early visual memory durability in infancy (Sanders & Johnson, 2021)*

- Investigate the age-appropriateness of a task battery composed of three unique infant VSTM tasks.
- Investigate the impact of increased delay duration (i.e., increasing cognitive load) on infant VSTM durability.
- Investigate age-related performance developments and correlations between performance on individual VSTM tasks.

Study 2: *Testing a memory account of the A-not-B error (Sanders & Johnson, 2021 [Under Review])*

- Investigate the relationship between infants' VSTM performance, as assessed with two age-appropriate tasks, and their A-Not-B error performance.

Study 3: *Neural correlates of infant visual short-term memory abilities*

- Investigate whether neural correlates of cognitive function, such as alpha and theta band power, are capable of distinguishing between higher and lower performing infants on a VSTM task.

Study 1

The goal of Study 1 was to systematically investigate the conditions in which early memory operates, including its scope and limits. Specifically, the effects of age and delay duration were examined in relation to VSTM performance, and performance was compared across three unique VSTM tasks. Here, a cross-sectional study is presented that examines developmental improvements in infant visual memory durability using a novel testing battery consisting of three tasks that have been previously investigated with infants: *Delayed Response* (Diamond & Doar, 1989), *Change Detection* (Oakes et al., 2006), and *Delayed Match Retrieval* (Kaldy et al., 2016). Infant memory was assessed using a battery of tasks to index the temporal boundaries and developmental growth of visual memory durability in the first postnatal year. This novel testing battery utilized a gaze-contingent eye tracking method and recorded infants' first fixations to target stimuli as the principal measure of performance.

Method – Study 1

Participants

Forty-nine healthy full-term infants ranging from 6-12 months ($M_{Age}=8.87$ months, $Median_{Age}=8.80$ months, $SD=1.75$, $Male=25$) participated in Study 1. Infants were recruited from the greater Los Angeles area from birth record lists provided by Los Angeles County. Each infant made a single visit to the lab where their performance was assessed on Delayed Response, Change Detection, and Delayed Match Retrieval tasks. An additional 10 infants were observed but not

included in the final sample from loss of data due to fussiness. Infants included in the final sample completed all trials for all tasks in the testing battery. The age breakdown of the final sample was as follows: 6-6.9 months (n=10), 7-7.9 months (n=9), 8-8.9 months (n=6), 9-9.9 months (n=7), 10-10.9 months (n=9), and 11-11.9 months (n=8). Families received a gift for their participation consisting of either a shirt, bottle, or small toy.

Eye Tracking Apparatus

An SR Eyelink 1000 eye tracking system with a 56 cm color monitor (SR Research Ltd.) was used to display stimuli and collect oculomotor data. Infants were seated on a parent's lap approximately 60 cm from the monitor. Prior to testing, each infant's point of gaze was calibrated using the standard calibration routine provided by the SR Eyelink software. The five-point calibration process began by presenting an attention-getting stimulus at the middle of the screen, as well as at each of the screens' four corners, as the infant looked toward each of the five locations in a random order. The experimenter controlled the calibration's progression by advancing to the next fixation location upon the infant's successful fixation to the current location. If the calibration result was poor for a particular fixation location, that calibration point was repeated until successful. Calibration was validated by presenting the same five stimuli at each of the five prior locations. If the validated fixations were within 1° visual angle error from the calibration fixations, the calibration was considered acceptable and the experimenter advanced to presentation of the eye tracking test battery. If the validation fixations did not meet this criterion, the calibration was repeated until this threshold was met.

Tasks within the test battery were programmed with Experiment Builder, the proprietary stimulus presentation software associated with the SR eye tracker. A separate computer was used to control stimulus presentation and send time-dependent markers to be stored with the eye

tracking data, allowing for the coordination of participants' eye movements with the respective stimuli. The eye tracking system recorded point-of-gaze coordinates (spatial resolution within 1.0° visual angle) at 500 Hz. Eye fixation locations and gaze durations to the whole scene as well as within specific areas of interest (AOIs) encompassing stimuli on the screen were recorded for each infant. Fixation triggers in the SR Experiment Builder software were utilized to implement gaze-contingency (a fixation within a specified AOI for a certain amount of time) to advance individual trials, thus providing automated scoring of memory performance based on infants' fixations.

Eye Tracking Test Battery

Delayed Response. Each trial began with a salient 'attention-getter' to re-center the infant's gaze on the screen (*see Figure 1*). Following this, a cueing stimulus appeared on either the left or right and remained on the screen for 1500 ms. Next, the re-centering attention-getter appeared for a variable duration (500 ms, 750 ms, 1000 ms, 1250 ms), followed by two identical colored shape targets appearing at both peripheral sides of the screen. If the infant first looked to the same side as the previously cued stimulus, the trial ended (contingent upon the infant's gaze to that location) and it was coded as a pass; otherwise, the trial ended after 1500 ms. Following the end of the trial, an attention-getter appeared and the next trial began. Eye-gaze data after delay periods were recorded and analyzed to determine if infants successfully maintained memories for cue stimulus locations. Infants were tested using 16 total trials split into four blocks with delay intervals of 500, 750, 1000, and 1250 ms. Task success was determined by whether the infant's first fixation was to the AOI of the correct previously-cued peripheral location, either on the left or right side of the screen. Thus, chance level performance in Delayed Response was 50% (left vs. right).

It is important to note that the implementation of Delayed Response had one significant departure from the traditional task. Delayed Response measures duration of memory for a hiding

event through the use of hiding wells, but this implementation instead utilized a disappearing cue. The use of a hiding event was avoided, as infants in the testing battery were already tested on two similar hiding event test procedures (implementations of the A-Not-B task using both real-world and virtual hiding wells).

Change Detection. Each trial began with an attention-getter centered on the screen (*see Figure 2*). Three same-sized, differently colored squares then appeared in random positions on the screen and remained visible for 5000 ms. Next, an attention-getter appeared for a variable delay, after which the array of squares re-appeared, one of which had changed color. The array remained on the screen for 5000 ms, or until the infant first fixated on the changed square, whereupon the display ended (i.e., contingent upon the infant's gaze to that location). Following the end of the trial, an attention-getter appeared prior to the beginning of the next trial. The trial was coded as a pass if the infant's first fixation was to the changed square. Positions of squares within the arrays were randomized for each trial. Infants were tested using 16 total trials split into four blocks with delay intervals of 500, 750, 1000, and 1250 ms. Task success was determined by whether the infant's first fixation was to the AOI of the changed square. Thus, chance level performance in Change Detection was 33.3% (square 1 vs. square 2 vs square 3).

It is important to note that this implementation of Change Detection had one significant departure from the traditional task. The traditional Change Detection task typically uses 500-1000 ms durations for encoding arrays, while this version utilized a 5000 ms encoding duration. A longer encoding period was chosen because infants did not perform successfully on the task during piloting with brief encoding durations.

Delayed Match Retrieval. Each trial began with an attention-getter centered on the screen (*see Figure 3*). Three face-down cards then appeared. Each card slid in from the side and remained

face-down for 1500 ms. The first card was then flipped face-up and remained on the screen for 2000 ms, followed by the second card in the same fashion. Next, the two face-up cards were flipped back face-down for 1000 ms. Once the cards were flipped face-down, they remained face-down for a variable delay, after which the card that was previously unexposed was flipped face-up and remained on the screen for 2000 ms. If the first fixation was to the corresponding face-down card, the infant was ‘rewarded’ with a small salient animation over the correct card, followed by an animation that brought the two cards together in a kiss, accompanied by a kissing sound (Kaldy et al., 2016), and the trial was coded as a pass. The kissing animation lasted for 5000 ms. If the infant’s first fixation was not to the matching face-down card, the two cards still ‘kissed’ to reinforce the rule for future trials, but the infant did not receive a salient animation. Following the end of the trial, the attention-getter appeared, and the next trial commenced. The Delayed Match Retrieval task requires observers to encode and maintain two relevant features (color, shape) for two cards, as well as their spatial locations, in memory. Therefore, infants are required to encode three stimulus features (color, shape, location) to succeed on the task. Infants were tested using 16 total trials split into four blocks with delay intervals of 500, 750, 1000, and 1250 ms. Task success was determined by whether the infant’s first fixation was to the AOI of the matching face-down card. Thus, chance level performance in Delayed Match Retrieval was 50% (face-up card 1 vs. face-up card 2).

It is important to note that this implementation of Delayed Match Retrieval had one significant departure from the traditional task. The traditional Delayed Match Retrieval task utilizes training trials, but this implementation did not. Training trials were not included in order to standardize the testing battery, as none of the other tasks in the battery utilized them.

General Eye Tracking Method

The eye tracking assessment was presented in a blocked fashion. Each block consisted of a single task and the order of tasks was counterbalanced for all infants (including the A-Not-B tasks not reported here) using a balanced Latin square. Each task was composed of 16 total trials, testing infants with four trials for each delay duration (500 ms, 750 ms, 1000 ms, 1250 ms). Thus, for each task, infants completed four trials for each delay in a randomized order.

Individual trials across all tasks were composed of three segments. The first segment introduced the stimuli to be encoded and stored in memory. The second segment served as a delay period: a black screen with a centered stimulus to re-orient attention (Delayed Response, Change Detection), or an interval during which cards were face-down (Delayed Match Retrieval). This variable delay period allowed us to test for maintenance of memory traces when delay duration is increased (see below). During the final segment, stimuli re-appeared and the infant's first fixation (100 ms minimum fixation duration) to the target stimuli was recorded. A time limit was imposed for each trial during the final segment (Delayed Response – 1500 ms, Change Detection – 5000 ms, Delayed Match Retrieval – 2000 ms) in which infants' responses were recorded and coded for one of three possible outcomes:

1. The trial was coded as a *pass* if the infant's first fixation was to the correct target stimulus' AOI (within the allotted time).
2. The trial was coded as a *fail* if the infant failed to make a first fixation to the correct target stimulus' AOI.
3. The trial was also coded as a *fail* if the infant never fixated on the correct target stimulus' AOI.

Memory Durability

Delay durations were directly manipulated within the tasks (500, 750, 1000, and 1250 ms)

to assess temporal limits of early visual memory durability. Delay durations were randomized within each task. The hypothesis was that average performance would decrease as delay duration increased.

Analysis

Each trial was binary-coded as either a pass (1) or fail (0), based on the infant's first fixation to the AOI of the correct target stimulus following the end of the delay period. Each task was composed of 16 trials split into four blocks, with each block consisting of four trials of each delay duration (500, 750, 1000, and 1250 ms). A combination of analyses—including t-tests to evaluate whether scores were different from chance levels, correlations, and logistic regressions—were utilized to test the different hypotheses.

To compare against chance levels, performance was operationalized as a ratio computed using the total number of passes vs. fails for each task and delay duration. For example, if an infant correctly fixated on three out of four 1250 ms trials in a task, their performance score for that task would be 0.75 for 1250 ms delays. For each task, average performance was computed across all ages for the various delay durations (*see Figure 4*). Deviations from chance level performance were computed for the effects of task type, delay duration, and age on performance using two-tailed one-sample *t*-tests with Bonferroni-adjusted *p*-values (please note that the reported alpha level should be compared to the provided Bonferroni-adjusted alpha level).

Results – Study 1

Chance Levels

Task Type. First, performance was examined for each task by collapsing across age and delay, and resulting *p*-values were compared to a Bonferroni adjusted alpha level of 0.0167 (3

comparisons). Average performance was significantly higher than chance levels (50%) for Delayed Response ($M=0.579$, $SD=0.161$, $t(48)=2.994$, $p=0.004$), significantly higher than chance levels (33.3%) for Change Detection ($M=0.545$, $SD=0.184$, $t(48)=8.09$, $p<0.001$), and not different from chance levels (50%) for Delayed Match Retrieval ($M=0.451$, $SD=0.250$, $t(48)=-1.364$, $p=0.179$).

Delay Duration. Next, the effect of increased delay duration on performance for each task was examined, collapsed across age, and resulting p -values were compared to a Bonferroni adjusted alpha level of 0.0125 (4 comparisons). For Delayed Response, infants performed significantly above chance levels (50%) for 500- ($M=0.618$, $SD=0.230$, $t(48)=3.61$, $p=0.001$) and 750 ms ($M=0.609$, $SD=0.250$, $t(48)=3.063$, $p=0.004$) delays, but performance did not differ from chance levels for 1000- ($M=0.553$, $SD=0.220$, $t(48)=1.675$, $p=0.100$) and 1250 ms ($M=0.493$, $SD=0.220$, $t(48)=-0.227$, $p=0.821$) delays. For Change Detection, infants performed significantly above chance levels (33.3%) for 500- ($M=0.529$, $SD=0.313$, $t(48)=4.395$, $p<0.001$), 750- ($M=0.599$, $SD=0.267$, $t(48)=6.96$, $p<0.001$), 1000- ($M=0.546$, $SD=0.305$, $t(48)=4.324$, $p<0.001$), and 1250 ms ($M=0.503$, $SD=0.276$, $t(48)=4.89$, $p<0.001$) delay durations. For Delayed Match Retrieval, performance did not differ from chance levels (50%) for 500- ($M=0.458$, $SD=0.430$, $t(48)=-0.676$, $p=0.502$), 750- ($M=0.505$, $SD=0.426$, $t(48)=0.648$, $p=0.521$), 1000- ($M=0.468$, $SD=0.421$, $t(48)=-0.949$, $p=0.350$), and 1250 ms ($M=0.468$, $SD=0.422$, $t(48)=-0.461$, $p=0.648$) delay durations.

Age. Lastly, developmental progression of task performance was examined by collapsing across delays, and resulting p -values were compared to a Bonferroni adjusted alpha level of 0.0083 (6 comparisons). For Delayed Response, infants did not perform different from chance levels (50%) at 6 ($M=0.463$, $SD=0.180$, $t(9)=-0.660$, $p=0.526$), 7 ($M=0.500$, $SD=0.108$, $t(8)=0.000$,

$p=1.000$), 8 ($M=0.583$, $SD=0.129$, $t(5)=1.581$, $p=0.175$), or 9 months ($M=0.598$, $SD=0.148$, $t(6)=1.754$, $p=0.130$). However, performance improved to marginally greater than chance by 10 ($M=0.632$, $SD=0.138$, $t(8)=2.873$, $p=0.021$) and 11 months ($M=0.668$, $SD=0.176$, $t(7)=2.708$, $p=0.030$). For Change Detection, infants performed marginally above chance levels (33.3%) at 6 ($M=0.475$, $SD=0.165$, $t(9)=2.729$, $p=0.023$) and 7 months ($M=0.486$, $SD=0.179$, $t(8)=2.567$, $p=0.033$). However, performance rose to significantly greater than chance levels by 8 ($M=0.552$, $SD=0.294$, $t(5)=1.824$, $p=0.003$), 9 ($M=0.613$, $SD=0.156$, $t(6)=4.741$, $p=0.003$), 10 ($M=0.542$, $SD=0.165$, $t(8)=3.786$, $p=0.005$), and 11 months ($M=0.633$, $SD=0.147$, $t(7)=5.757$, $p=0.001$). For Delayed Match Retrieval, infants did not perform greater than chance levels at any age (6 months: $M=0.471$, $SD=0.258$, $t(9)=-0.357$, $p=0.729$; 7 months: $M=0.338$, $SD=0.262$, $t(8)=-1.858$, $p=0.100$; 8 months: $M=0.572$, $SD=0.295$, $t(5)=0.596$, $p=0.577$; 9 months: $M=0.441$, $SD=0.288$, $t(6)=-0.544$, $p=0.606$; 10 months: $M=0.508$, $SD=0.205$, $t(8)=0.114$, $p=0.912$; 11 months: $M=0.459$, $SD=0.175$, $t(7)=-0.670$, $p=0.524$).

Correlations

Correlations were calculated between age and individual task performance, as well as for performance between each task. (Corrections for multiple comparisons were not made for correlational analyses, as correlational data was investigated for exploratory and informational purposes.) Overall, infants' performance between individual tasks was not correlated. Specifically, Delayed Response performance was not correlated with Change Detection performance ($r=0.136$, $p=0.352$) or Delayed Match Retrieval performance ($r=0.145$, $p=0.319$), and Change Detection performance was not correlated with Delayed Match Retrieval performance ($r=0.038$, $p=0.798$). However, there were significant correlations between age and performance for two tasks: Delayed Response ($r=0.461$, $p=0.001$) and Change Detection ($r=0.309$, $p=0.031$). The correlation between

age and Delayed Match Retrieval performance was not significant ($r=-0.001$, $p=0.995$). Scatterplots were produced to visualize the relation between age and performance (see Figure 5).

Correlations were also conducted between age and individual task performance for each delay duration (see Figure 6). Infants' Delayed Response performance was significantly correlated with age for 500- ($r=0.367$, $p=0.009$), 750- ($r=0.319$, $p=0.025$), and 1250 ms ($r=0.373$, $p=0.008$) delays, but not for 1000 ms ($r=0.208$, $p=0.151$) delays. Infants' Change Detection performance was significantly correlated with age for 500 ms ($r=0.312$, $p=0.029$) delays, but not for 750- ($r=0.007$, $p=0.960$), 1000- ($r=0.182$, $p=0.211$) or 1250 ms ($r=0.265$, $p=0.065$) delays. Infants' Delayed Match Retrieval performance was not correlated with age for 500- ($r=0.024$, $p=0.871$), 750- ($r=0.022$, $p=0.884$), 1000- ($r=-0.035$, $p=0.815$), or 1250 ms ($r=0.017$, $p=0.908$) delays.

Generalized Linear Mixed Model

To compare performance across the different tasks, delays, and ages (i.e., to determine the extent to which task, delay duration, and age predicted performance), the data were modeled using a Generalized Linear Mixed Model (GLMM) with logit function and a covariance structure including random intercepts. A GLMM was chosen in order to accommodate for delays being nested within tasks, and tasks being nested within infants. This analysis was most appropriate for this dataset because the dependent measure for each trial was a binary outcome and GLMM allows for use of both quantitative and qualitative predictor variables using logistic regressions. The predictor variables included were: task type (Categorical: Delayed Response, Change Detection, Delayed Match Retrieval), delay duration (Categorical: 500 ms, 750 ms, 1000 ms, 1250 ms), and age (Continuous: months). The dependent variable, performance, was computed by the model using each infant's total number of binary-coded passes for each trial as the numerator and number of possible trials as the denominator.

Task Type. Average performance across tasks was compared in terms of log odds from the logit distribution. The results of the GLMM fixed effects output indicated that task type ($F(2,529)=5.512, p=0.004$) was a significant predictor of performance. Performance differences were most apparent when contrasting Delayed Match Retrieval and Delayed Response; specifically, performance significantly increased the log odds by 0.483 ($p=0.001, SE=0.146, 95\% CI=[0.197-0.769]$) when tested against Delayed Response. When comparing performance on Delayed Match Retrieval to Change Detection, performance significantly increased the log odds by 0.390 ($p=0.012, SE=0.155, 95\% CI=[0.086-0.694]$) when tested with Change Detection. (*see Table 1 for the full set of contrasts*)

Delay Duration. Average performance across delays was compared in terms of log odds from the logit distribution. The results of the GLMM fixed effects output indicated that delay duration ($F(3,216)=3.938, p=0.009$) was a significant predictor of performance. Performance differences were most apparent when contrasting delays of 750 ms and below and delays of 1000 ms and above. Specifically, log odds increased by 0.243 when comparing performance on 1250- vs. 500 ms trials ($p=0.068, SE=0.133, Odds Ratio=1.275, 95\% CI=[-0.018-0.504]$), and increased by 0.388 when comparing 1250- vs. 750 ms trials ($p=0.005, SE=0.136, 95\% CI=[0.121-0.655]$). In contrast, log odds only increased by 0.060 on 1250- vs. 1000 ms trials ($p=0.647, SE=0.132, 95\% CI=[-0.198-0.319]$). (*see Table 1 for the full set of contrasts*)

Age. The results of the GLMM fixed effects output indicated that age ($F(1,446)=20.457, p<0.001$) was a significant predictor of performance. The coefficient associated with the continuous age predictor revealed that for every 1 month increase in age, the log odds of passing a given trial significantly increased by 0.136 across all tasks and delays ($p<0.001, SE=0.027, 95\% CI=[0.081-0.190]$).

Discussion – Study 1

Study 1 is the first to assess infants' performance on a visual memory task battery with the goal of indexing the scope, temporal boundaries, and development of early memory abilities in the first postnatal year. Two key components of infant visual memory were investigated—durability and developmental trajectories—using three unique tasks, and the results help inform the understanding of how memory durability improves in infancy and how it may be quantified in early development.

Age-Appropriateness

The first goal of Study 1 was to assess the age-appropriateness of each VSTM task (Delayed Response, Change Detection, and Delayed Match Retrieval) by comparing relative performance against chance levels. This was accomplished using two-tailed one-sample *t*-tests with Bonferroni adjusted *p*-values to correct for multiple comparisons. The fixed effects GLMM output also indicated that task type significantly predicted performance across the entirety of the testing battery, over and above the other variables.

Collapsed across age and delay, average performance was significantly higher than chance levels for Delayed Response. As suggested by previous literature, Delayed Response appears to be an appropriate test of early memory durability. For Delayed Response, infants must encode the spatial location of a single previously presented visual cue stimulus varying between one of two possible locations (left or right). Success also requires the inhibition of a pre-potent response to look to the previously presented location, if it was different, and instead use memory to guide oculomotor behavior to the new location. However, at closer glance, this adaptation of Delayed Response can also be viewed as an attentional cueing task, requiring minimal memory demands (Fan et al., 2002) and instead reflecting exogenous cueing of spatial attention (Ross-Sheehy et al.,

2015). As mentioned previously, this discrepancy stemmed from the decision to forgo using hiding wells and instead using a disappearing cue. Without the use of hiding wells, this implementation provides no information that the object continues to exist once occluded. On this account, infants do not necessarily have to bind a particular shape to a specific location for successful performance, rather, the abrupt cue onset may automatically capture attention to that spatial location. This may leave a lingering attentional trace at that location, prime that location, or bring it into some privileged state where the infant finds it more interesting; thus, attention may have been captured at that location and it remained there. In this case it may not be the memory of the cue's location that fades away with time, but the extent to which it signals that something interesting will be presented on that side. An analogy is to consider when your cellular phone makes a noise when receiving an incoming message. You only have a few seconds to check the message displayed on the screen before it dims, but if you do not look at the message, it is not the result of having forgotten there was a noise. Therefore, although memory may still be required to succeed on the task, the aforementioned attentional confounds cannot be ruled out as contributing to Delayed Response performance.

Collapsed across age and delay, average performance was also significantly higher than chance levels for Change Detection. As suggested by previous literature, Change Detection also appears to be an appropriate test of early memory durability. However, it is important to note that average performance (54.5%) was slightly lower (*see Figure 4*) when compared to Delayed Response (57.9%), perhaps because the Change Detection task was more cognitively demanding. For Delayed Response, the object's location is the only relevant stimulus feature to be encoded; therefore, maintenance of other stimulus features (such as the cue stimulus' color or shape) is not required for successful performance. However, during each Change Detection trial, infants are

required to encode colors and spatial locations of three individually colored squares and retain that memory over the delay. Following the delay, infants must again encode the new array of three squares and identify the changed square by comparing new information with previously encoded information held in memory. Infants must encode the color of each square as well as their respective spatial locations in the array—two features (color, location) for each item—as opposed to one feature (location) in Delayed Response.

It is also important to note that the use of this testing battery has been emphasized for investigating shorter-term visual memory processes, but the 5000 ms encoding familiarization period utilized in this Change Detection task may have been long enough to tap longer-term memory systems. Thus, successful performance may have also been driven by ensemble processing (e.g., mean color change across arrays) and allocation of global attention (Brady & Tenenbaum, 2013; Pailian & Halberda, 2015). The longer encoding period may have also allowed for two critical attentional processes that could both influence performance beyond just the use of STM: (1) fixation of each square in the encoding array and (2) sufficient time to encode the entire array (either piecemeal or holistically) into longer-term memory. Since infants' developing attention skills may influence their ability to rapidly disengage and re-fixate in the context of virtual competition, and since fixations to specific items during encoding are likely to facilitate memory, these age-related findings may also represent a capacity-like pattern of visual attention. This possibility was addressed with a follow-up analysis. Each infants' total number of fixations during the 5000 ms encoding period were calculated and included as the outcome variable in a regression model with age as the predictor. The overall regression model was significant ($R=0.335$, $R^2=0.112$, $R^2_{Adj}=0.095$, $df=1$, $MS=3458.515$, $F=6.327$, $p=0.015$), with age significantly predicting the total number of fixations during the encoding period ($B=4.386$, $SE=1.744$, $t=2.515$, $p=0.015$).

Thus, as infants age, they make significantly more fixations during the encoding period, providing evidence that attention and longer-term memory may additionally influence infant performance in the Change Detection task, beyond just the use of STM abilities. (Due to the gaze-contingent nature of this measure, we were unable to examine preference for the changed square as a function of looking to the entire test array, since the test interval ended if the first fixation was to the changed square.) Tasks that aim to investigate shorter-term memory processes typically incorporate brief encoding durations of less than a second. As mentioned earlier, a longer encoding period was chosen for this task because piloting revealed that infants often did not succeed until they were given 5000 ms to respond. The range of delays over which Study 1 examined memory durability, therefore, may involve both short- and long-term storage mechanisms. This remains a question for future research.

Collapsed across age and delay, average performance did not differ from chance levels for Delayed Match Retrieval. This task was likely the most cognitively demanding in the battery, because infants must encode three relevant features (shape, color, location) of two cards to maintain in memory over a delay until the third card is exposed. Once exposed, the third card must also be encoded and compared with stored memories of the two face-down cards. In this respect, Delayed Match Retrieval may prove to be an exceptionally challenging task for infants, suggesting that more advanced memory processes may be needed for successful performance (such as planning or reasoning). For example, Delayed Match Retrieval requires infants to make online predictions over multiple locations based on remembered information (Kaldy et al., 2016, p. 897).

Notably, no evidence was obtained for successful Delayed Match Retrieval performance even in the oldest infants observed (up to 12 months), in contrast to successful performance at 10 months as reported by Kaldy et al. (2016). Part of the explanation for this discrepancy may stem

from the testing battery requiring multiple assessments, which is likely to place additional demands on infants' attentional and cognitive resources, and thus perhaps impairing overall performance. Nevertheless, results from Delayed Response and Change Detection tasks reflect substantial differences in performance as a function of task and age, implying that this testing battery was not overly demanding. In addition, Kaldy utilized training trials in the original version of the task, while Study 1 did not. As mentioned earlier, these were not included in order to keep the tasks standardized across the testing battery, but training may be necessary for the memory effect, due to the complex causal structure of the task. (Nevertheless, this adaptation of the task reinforced learning of the causal structure. The matching cards always kissed at the end, similar to the original task, and infants received a salient reward animation when they made a correct fixation.) Successful performance on the Delayed Match Retrieval task, therefore, may rely on cognitive resources other than memory for matching face-down cards because infants also presumably learn that the correct match will be followed by something interesting (the salient animation).

Memory Durability

The second goal of Study 1 was to assess the scope of early visual memory durability by examining the effect of increasing temporal delay on performance across tasks. This was accomplished by comparing average performance across various delay periods to chance levels, as well as by examining the delay duration fixed effect output from the GLMM output.

For Delayed Response, infants performed significantly above chance levels across delay durations of 500 and 750 ms, but performance did not differ from chance for the highest delays of 1000 and 1250 ms. However, for Change Detection, infants performed significantly above chance levels across all delay durations, suggesting that the range of delay durations chosen did not significantly impact performance. This performance discrepancy may stem from developmental

timings within different brain regions. Change Detection performance may rely on the posterior parietal cortex (Tseng et al., 2012), while Delayed Response performance may rely more on frontal regions (Diamond & Doar, 1989), which generally mature at a slower rate than the parietal regions. Therefore, memory durability is stronger for Change Detection than Delayed Response in part because posterior parietal cortex is relatively more functional in infants than the frontal lobe. For Delayed Match Retrieval, performance did not differ from chance levels across all delay durations.

Performance Across Tasks

Performance across tasks was not correlated for individual infants. As noted earlier, this may be due to the possibility that Change Detection and Delayed Response performance relies on maturation of different brain regions. The Change Detection, Delayed Response, and Delayed Match Retrieval tasks thus may test distinct kinds of visual memory, though their precise nature remains to be discovered. As noted, the three tasks may also pose distinct cognitive demands over the same four delay durations.

Developmental Trajectories

The final goal was to quantify the development of visual memory durability between 6 and 12 months. This was accomplished by: (i) comparing age-related performance across individual tasks to chance levels, (ii) examining GLMM output related to age, and (iii) examining R^2 linear values between age and performance obtained via correlation analyses.

For Delayed Response, infants' performance was not marginally different from chance until 10 months. For Change Detection, performance was marginally above chance starting from 6 months, was significantly greater than chance by 8 months, and continued to improve. For Delayed Match Retrieval, infants did not perform different from chance levels at any ages. Regarding the GLMM output, the fixed effect associated with age revealed that for every 1 month

increase in age, the odds of passing a given trial across the testing battery significantly increased, suggesting that older infants were more likely to perform successfully across the task battery.

Developments in performance were also examined by collapsing across delays and examining the relation between age and individual task performance based on R^2 linear values obtained from the correlation analyses. Examining these values allowed us to determine the percent of variability that age accounted for in performance for each task. For Delayed Response, collapsed across delays, there were linear increases in average performance from above 40% at 6 months to above 60% at 12 months. For Change Detection, average performance also increased linearly from above 40% at 6 months to above 60% at 12 months. For Delayed Match Retrieval, average performance showed no age-related changes from 6 to 12 months. As shown in Figure 5, the percent of variability accounted for by age in each task was as follows: Delayed Response (21.3%), Change Detection (9.5%), and Delayed Match Retrieval (<0.01%). These results provide evidence, therefore, for significant age-related improvements in Delayed Response and Change Detection performance, but not in Delayed Match Retrieval, between 6 and 12 months of age. Furthermore, significant correlations were found between age and performance for Delayed Response and Change Detection (indicating age-related improvement in both), but not for Delayed Match Retrieval.

Finally, age-related developments in performance were examined for individual delays between tasks as shown in Figure 6. R^2 linear values obtained from the correlation analyses were examined to determine the percent of variability that age accounted for in performance for each delay duration between tasks. For Delayed Response, age was significantly related to performance on 500, 750 and 1250 ms delays, but not for 1000 ms delays. For Change Detection, age was significantly correlated with performance for only 500 ms delays, but not for higher delays. For

Delayed Match Retrieval, age was not correlated with performance for any delay periods.

Conclusions – Study 1

Study 1 provides new insights about fundamental memory abilities in infancy. It provided evidence that infants begin to perform marginally above chance on memory paradigms beginning from 6-7 months with robust improvements across tasks by 10 months. It also provides evidence regarding infant memory durability: longer delays between 500-1250 ms significantly hindered performance. In addition, this study provides important tools for future research of infant memory durability. For example, the distinct nature of infants' performance in Delayed Response and Change Detection tasks may help shed light on development of different brain systems that subserve memory, in this case posterior parietal cortex and frontal areas. Despite the methodological departures highlighted when creating the tasks limit the ability to draw firm conclusions regarding the use of VSTM mechanisms, results nonetheless make a substantial contribution to the literature, by providing the first-ever cross-task assessment of the joint influence of attention, VSTM, and LTM as a function of delay interval.

Study 2

Taken together, previous studies suggest that successful search in the A-Not-B task may possibly be explained by memory abilities (Cummings & Bjork, 1983a, 1983b), yet no study to date has provided a clear test of this hypothesis by testing A-Not-B error performance and VSTM performance in the same group of infants. In Study 2, a group of 6-12-month-olds were observed with a looking A-Not-B task and two age-appropriate VSTM tasks, Delayed Response and Change Detection, and relations in performance were analyzed. The reasoning was that if looking A-Not-B error performance was a reliable assessment of infant memory abilities, individual differences in success on the A-Not-B task would be found that were significantly correlated with individual

differences in memory performance across VSTM tasks.

Method – Study 2

Participants

Forty-nine healthy full-term infants from 6-12 months ($M_{Age}=8.87$ months, $Median_{Age}=8.80$ months, $SD=1.76$, $Male=25$) participated in Study 2 (same infants from Study 1). Each infant made a single visit to the lab and were assessed with two VSTM assessments (Delayed Response and Change Detection, Gilmore & Johnson, 1995; Oakes et al., 2013; Ross-Sheehy et al., 2003; Sanders & Johnson, 2021; Schwartz & Reznick, 1999), and an oculomotor version of the A-Not-B task. Data from three infants were excluded due to fussiness. Infants included in the final sample completed all trials for all tasks. Families received a gift for their participation consisting of a shirt, bottle, or toy.

Eye Tracking Acquisition

The eye tracking acquisition process was the same as Study 1.

VSTM Tasks

Delayed Response. The task procedure of Delayed Response was the same as Study 1.

Change Detection. The task procedure of Change Detection was the same as Study 1.

A-Not-B Task

In the A-Not-B task, a set of toy keys was shaken in the top-center of the screen along with a rattling noise (see Figure 7). The keys then moved diagonally toward one of the two hiding locations, grey squares on the bottom left and right sides of the screen. Once the keys moved behind a square, an attention-getter stimulus appeared in the top-center for 3000 ms to break the infant's gaze to the hiding locations. The attention-getter then disappeared and infants' looking

behaviors to the two on-screen hiding locations were recorded and analyzed. For the first two trials, the keys were always hidden in the same location (A), and for the third trial, the keys were always hidden in the remaining location (B). Left-right locations of A and B were randomized for each infant. Infants always advanced to the third B-trial regardless of their performance on A-trials.

Performance was coded as “successful” if the first fixation was to the correct AOI (Location B) during the third trial, after making (correct) first looks to Location A on trials 1 and 2. Performance was coded as a “fail” if the first fixation during the third trial was toward the incorrect Location A or toward the incorrect Location B on trials 1 and 2. A time limit (4000 ms) was imposed for each trial following the delay period, whereupon the display ended (i.e., contingent upon the fixation to that location). Half the infants were first observed in the A-Not-B task followed by the Delayed Response and Change Detection tasks (order counterbalanced), and half were tested with A-Not-B subsequently.

Analysis

For the A-Not-B task, first-gaze fixations to the two hiding locations after delay periods were coded for correct or incorrect responses, and differences in ages were analyzed using t-tests. To determine the extent to which age and performance on the Delayed Response and Change Detection tasks predicted A-Not-B performance, data were modeled using logistic regression (GLMM was not utilized as in Study 1 due to the effect of delay duration not being analyzed for). The predictor variables included were age (Continuous: months), Delayed Response performance (Continuous: Proportion correct of 16 trials collapsed across delay durations), and Change Detection performance (Continuous: Proportion correct of 16 trials collapsed across delay durations). The outcome variable was looking A-Not-B error performance (Binary: pass/fail).

Results – Study 2

Twenty-eight (57.1%) of the 49 infants succeeded on the A-Not-B task, making their first fixation to the correct B location on the third trial after fixating to the correct A location on trials 1 and 2. The mean ages of infants who displayed the error (8.560 months, $SD=1.720$) or who succeeded (9.100 months, $SD=1.790$) were not significantly different ($t(47)=-1.060, p=0.295$).

The results of the logistic regression were not significant for any predictor variables; neither age ($B=0.066, SE=0.192, df=1, p=0.732, Exp(B)=1.068$), average Delayed Response performance ($B=0.064, SE=2.012, df=1, p=0.975, Exp(B)=1.066$), nor average Change Detection performance ($B=-0.308, SE=1.654, df=1, p=0.852, Exp(B)=0.735$) predicted the A-Not-B error. No difference was found in performance on Delayed Response ($t(47)=-0.185, p=0.854$) or Change Detection ($t(47)=0.066, p=0.948$) for infants who participated in the A-Not-B task prior to or after one of the VSTM assessments.

Discussion – Study 2

Some theories have attributed infants' A-Not-B error to fragile VSTM (Cummings & Bjork, 1983a, 1983b), while others have attributed it to other factors such as motor reaching habit (Smith et al., 1999) or social reward cues (Topál et al., 2008). Study 2 is the first to directly compare infants' looking A-Not-B error performance with their cognitive VSTM performance, assessed via two unique age-appropriate eye tracking tasks. The Delayed Response task requires maintaining a representation of a stimulus's spatial location in memory, whereas the Change Detection task requires maintaining representations of three squares' locations and colors in memory. These tasks have been used in the past as markers of infant VSTM (Gilmore & Johnson, 1995; Oakes et al., 2013; Ross-Sheehy et al., 2003; Sanders & Johnson, 2021; Schwartz &

Reznick, 1999), and have been shown to be valid age-appropriate measures that index the ability to maintain a representation of an object and its location in memory. Utilization of these tasks in combination provided a direct test of the possibility that individual differences in VSTM abilities may serve as an explanation of infants' A-Not-B error performance.

Infants' VSTM performance as assessed by Delayed Response or Change Detection tasks showed no relation to oculomotor A-Not-B performance, and this implies that other factors are important for understanding correct or incorrect search on the crucial B-trial. This is somewhat counterintuitive, because success on the A-Not-B task requires infants to visually track the virtual set of keys as it was being hid into each hiding location and remember which location it was. All the infants watched the keys disappear into Location B, but once their attention was broken, many infants still made perseverative first looks back to Location A on the B-trial following the delay.

These results might be best explained with an inhibitory control account (Diamond, 1990a) according to which infants demonstrating the A-Not-B error may possess a strong memory for Location A that is difficult to inhibit during B-trials; the tendency to make the error may be exacerbated with use of a 3000 ms delay duration. Conversely, infants who succeeded at the A-Not-B task may possess more advanced inhibitory control abilities than their same-aged peers, based on their ability to make a correct first look to Location B. This finding is notable, because some infants searched incorrectly on the B trial even though it required no reaching responses and had no social cues/rewards. Diamond interpreted infants' perseverative reaches in terms of an immature dorsolateral prefrontal cortex (DLPFC) (Diamond, 1990a). The DLPFC, part of the anterior attention system, is thought to allow for the development of inhibitory control, facilitating more precise control over voluntary visual fixations (Posner & Petersen, 1990). Specifically, infants at 6-9 months begin to inhibit their attention to distracting stimuli (Amso & Johnson, 2005,

2008), and this may support cognitive skills such as object segmentation and perception of object occlusion (Amso & Johnson, 2006; van Renswoude et al., 2019). Oculomotor inhibition may be particularly important in directing infants' attention following a delay period. Results of Study 2 are consistent with the likelihood that the DLPFC and anterior attention system may still be immature up to 12 months. In addition, results demonstrate that some infants produce oculomotor perseverative search, in parallel with results when reaching is the dependent measure (Smith et al., 1999).

However, VSTM abilities are clearly important for success on the A-Not-B task. To succeed on the first two Location A trials, infants must retain the correct hiding location in memory during the delay. The accumulated memories formed after two consecutive correct searches at Location A coupled with immature inhibitory control increased the likelihood of a perseverative first look toward Location A. This comes at somewhat of a surprise, since this implementation of A-Not-B did not utilize any training trials, and was composed of solely three trials: two Location A trials and one Location B trial. Nevertheless, two consecutive A-trials seemed to be enough to draw attention back to Location A on the critical B-trial. It is also surprising that Delayed Response task performance did not predict performance on A-Not-B, as the two tasks are conceptually similar (Diamond, 1990a). It is important to note that this implementation of Delayed Response did not involve the use of hiding wells or the same type of visual scanning that is used in more common implementations (Bell & Adams, 1999; Butterworth, 1977; Clearfield et al., 2006; Diamond, 1990), as the disappearing cue utilized provided no information that the object continues to exist once it disappears.

Although VSTM improves as infants mature (Hofstadter & Reznick, 1996; Pelphrey et al., 2004; Ross-Sheehy et al., 2003; Sanders & Johnson, 2021), there was no relation found between

age and A-Not-B performance, again suggesting that infants as old as 12 months may not possess sufficient inhibitory control to overcome memories for successful search at two consecutive Location A trials. Future studies should further explore the relation between A-Not-B error and infant inhibitory processes with an age-appropriate oculomotor task battery to index individual differences in inhibition abilities and infant A-Not-B error performance.

Conclusions – Study 2

In conclusion, Study 2 provides evidence that infant VSTM abilities, as indexed via two unique tasks, did not predict oculomotor A-Not-B performance in a sample of 6–12-month-olds. Infants who make perseverative looks back to Location A following a delay may be unable to inhibit the tendency to return attention to Location A, even after seeing the object hidden at Location B, and infants who succeed on the task may possess more advanced inhibitory control abilities that allow them to suppress the urge to look back to Location A. Further evidence that VSTM and A-Not-B performance may not be directly related comes from previous findings that infants produced the A-Not-B error on reaching versions with the object fully visible (Butterworth, 1977) as well as uncovered (Bremner & Knowles, 1984; Piaget, 1955), and that performance is known to be susceptible to constraints on spatial coding independent of memory (Bremner, 1978; Bremner & Bryant, 1977). Infants' looking A-Not-B error performance, therefore, likely reflects some aspect of memory, as noted previously. Correct looks to Location A require the use of VSTM, while correct looks to Location B require not only the use of VSTM, but also inhibitory control.

Study 3

Previous studies with older children and adults have suggested that neural correlates of cognitive function, such as alpha and theta band power, may be useful for studying individual

differences that underlie memory performance throughout development (Bache et al., 2015; Clark et al., 2004; Klimesch, 1997, 1999; Klimesch et al., 2006; Klimesch et al., 1997; Klimesch et al., 1993; Krause et al., 2008; Stam, 2000; Werkle-Bergner et al., 2006). However, no study yet has closely investigated the relationship between alpha desynchronization, theta synchronization, and VSTM performance in infancy. Here a direct examination is presented, investigating neural correlates of successful oculomotor memory performance using an age-appropriate infant VSTM task while manipulating temporal cognitive load. In Study 3, individual variability in neural alpha and theta activity was examined as to how they modulated performance for higher and lower performing infants on the Change Detection task. It was hypothesized that higher performing infants would display greater levels of alpha desynchronization and theta desynchronization, relative to lower performers. High-density 128-channel EEG was recorded from infants at a 500 Hz sampling rate to closely investigate neural correlates underlying VSTM performance in typically developing 8-month-olds.

Method – Study 3

Participants

Ten healthy full-term 7.5-8.5-month-old infants from the greater Los Angeles area were recruited from a university participant database (a different sample of infants from Studies 1 and 2). (This age range was chosen based on results of Study 1, revealing that VSTM performance assessed by Change Detection may be operational at 8-months-old.) Data collection was halted prematurely due to the COVID-19 pandemic. Four infants were dropped from the analysis because of fussiness resulting in insufficient EEG data. The final sample consisted of six infants ($M_{Age}=8.38$ months, $Male=4$). Each infant made a single visit to the UCLA Baby Lab where they were assessed

on a resting-state baseline EEG measure and a cognitive EEG measure while participating in the Change Detection task.

Eye Tracking Acquisition

The eye tracking acquisition procedure was the same as Studies 1 and 2.

Change Detection

The Change Detection task procedure was the same as Studies 1 and 2, except that different delay durations were utilized. The impact of increasing delay duration on Change Detection performance was examined by varying the temporal delays at which infants were required to maintain information in memory. Trials varied with respect to specific delay durations imposed to manipulate memory durability demands (100- and 3000 ms) (Kwon et al., 2014; Oakes et al., 2013; Oakes et al., 2011; Oakes et al., 2006; Ross-Sheehy et al., 2003; Simmering, 2012). By varying delay duration, links between neural band power and VSTM performance modulated by increased cognitive load could be further investigated. Specifically, it was hypothesized that higher performers and lower performers could be further differentiated by examining behavioral performance between the two delay durations. The 3000 ms delay was chosen to expand on results from Study 1, where 8-month-olds were shown to perform above chance levels on Change Detection trials with 500–1250 ms delays.

EEG Acquisition

A Net Station NetAmps 300 EEG amplifier (Phillips Inc.) was used to record continuous high-density 128-channel EEG brain activity at a frequency of 500 Hz. EEG was continuously recorded from each infant while they participated in a resting-state baseline measure and a task-state cognitive measure.

Resting-State. A continuous 2-minute EEG recording of baseline resting-state brain activity was recorded before infants participated in the Change Detection task. The resting-state baseline measure was recorded prior to the task-state measure because piloting revealed that infants were most calm at this point in the experiment, and most representative of a baseline resting-state. During resting-state recordings, infants viewed a video of bubbles bouncing slowly on the screen in silence.

Task-State. A continuous EEG recording of Change Detection task-state brain activity was recorded after infants participated in the baseline resting-state recording. Infants participated in 24 Change Detection trials displayed on the screen.

Procedure

Infants made a single visit to the UCLA Baby Lab. Upon arrival, their head was measured to determine the appropriate size of EEG cap used for recording. Infants were placed on their caregiver's lap seated across from an eye tracker equipped monitor. A high-density 128-channel EEG cap was soaked in a solution of warm water, potassium chloride, and baby shampoo. After 10 minutes of soaking, the EEG cap was placed on the infant's head by an experimenter and assessed for proper fit. High impedances for single channels were resolved via re-application of solution to individual electrodes. A target sticker was placed on top of a frontal electrode (#17) to aid the eye tracker in its calibration process. Lights were turned off and infants first participated in a resting-state baseline recording, viewing a video of bubbles bouncing on the screen for 2 minutes in silence. Following the resting-state recording, infants participated in the eye tracking calibration process as per Studies 1 and 2. Once the eye tracker was calibrated, infants participated in 24 Change Detection trials. Once finished, the experimental session was complete and the EEG cap was removed from the infant's head.

Eye Tracking Data Preparation

Eye tracking data from the Change Detection task were inspected using DataViewer, an SR proprietary software (SR Research Ltd). First fixations after delay periods were recorded and analyzed for whether infants attended to the correct changed square, which resulted in a binary coded behavioral outcome variable for each trial. Change Detection consisted of 24 total trials varying between two delay durations: 12 trials of 100 ms delays and 12 trials of 3000 ms delays. VSTM performance at each delay duration was calculated as the total number of correct trials out of 12 possible for each delay duration.

EEG Data Preparation

EEG data were processed and analyzed using EEGLAB, a MATLAB plugin (Delorme & Makeig, 2004). The EEGLAB data cleaning pipeline included the following steps in chronological order:

1. *Bandpass Filtering*. Raw EEG data were bandpass filtered from 0.1-50 Hz, excluding frequencies below 0.1 Hz and above 50 Hz.
2. *Bad Channel Cleaning*. Filtered EEG data were then manually cleaned via visual inspection for bad channels.
3. *Bad Channel Interpolation*. Bad channels removed from the cleaned EEG data were then interpolated using information from neighboring electrodes.
4. *Average Re-Reference*. The EEG data were then average re-referenced, typical in studies using high-density EEG (Dien, 1998).
5. *Independent Component Analysis (ICA)*. The EEG data were then processed using ICA to remove any non-neural artifacts, such as blinks, saccades, and muscle activity (Fujioka et al., 2011). Since ICA does not remove any EEG data, the amount of data input into ICA is the same as the amount of data output.

Band Power. After continuous EEG data were processed, FFT was performed on the time series data. The filtered spectrum from 0.1–50 Hz was examined for two infant frequency bands: theta (2.0–5.9 Hz) and alpha (6.0–9.0 Hz), as defined in previous studies (Bell, 2012; Cuevas et al., 2012; Marshall et al., 2002; Reynolds & Romano, 2016; Xie et al., 2018). In order to investigate whether certain brain regions were particularly responsible for driving neural band power, three different neural regions of interest were chosen: *frontal*, *midline*, and *posterior*. Furthermore, each brain region was further broken down into 3 sub-regions: *left*, *mid*, and *right*. This resulted in 9 different possible neural areas of interest: *left-frontal*, *mid-frontal*, *right-frontal*; *left-midline*, *mid-midline*, *right-midline*; *left-posterior*, *mid-posterior*, *right-posterior*. (See Table 2 and Figure 8 for representations of electrodes chosen for specific regions and subregions.) Absolute power was calculated for each electrode of interest in each frequency band by squaring the amplitude of the individual frequency components. FFT was performed separately for resting-state and task-state recordings.

Synchronization / Desynchronization. Theta synchronization and alpha desynchronization analyses proceeded after FFT was performed and power values were extracted. Synchronization and desynchronization correspond respectively to the percentage of power increase or decrease in each frequency band during a cognitive task-state, relative to a baseline resting-state. Analyses began by comparing mean power values for each frequency band from Change Detection (task-state) to those from baseline (resting-state), and was calculated according to the following formula (Pfurtscheller & Aranibar, 1977):

$$\frac{\text{Band Power}_{(\text{Resting-State})} - \text{Band Power}_{(\text{Task-State})}}{\text{Band Power}_{(\text{Resting-State})}} * 100\%$$

This calculation's outcome yielded either a positive (desynchronization) or negative (synchronization) percent change for alpha and theta task-state power, relative to resting-state power. To clarify, if an infant exhibited higher levels of resting-state alpha power and lower levels of task-state alpha power, this infant would be displaying alpha desynchronization. On the other hand, if an infant exhibited lower levels of resting-state theta power and higher levels of task-state theta power, this infant would be displaying theta synchronization.

Analysis

The effect of increased delay duration on VSTM performance was tested using a dependent samples t-test, comparing performance between 100- and 3000 ms trials. Correlation analyses examined relationships between infants' oculomotor and electrophysiological data. Performance on Change Detection was defined by collapsing across delay durations and totaling the number of correct trials out of 24. Linear regressions were used to further analyze significant correlations between infants' Change Detection performance and alpha desynchronization. The regression model included alpha desynchronization and theta synchronization as predictors, with the outcome being infants' Change Detection performance.

Results – Study 3

Change Detection Performance

Delay Duration. Results indicated no effect of delay duration for the number of trials correct ($t(10)=-0.705, p=0.497$), with infants averaging 5.670 ($SD=3.445$) correct trials for 100 ms delay periods and 6.830 ($SD=2.137$) correct trials for 3000 ms delay periods. Because no effect of delay duration was found, trials for further analyses were collapsed across the two delay periods in order to preserve maximum statistical power. On average, infants performed correctly on 12.5

trials (52.08%) of 24 possible, which was significantly higher than chance (33.3%) performance ($SD=0.141$, $t(5)=3.251$, $p=0.023$).

EEG Data Analyses

Descriptives. (See Tables 3 and 4 for a list of alpha and theta power descriptive statistics.)

Correlations. Significant correlations were found between Change Detection performance and: (1) average alpha desynchronization (see Figure 9), (2) average frontal alpha desynchronization (see Figure 10), and (3) average right posterior alpha desynchronization (see Figure 11). No significant correlations were found between Change Detection performance and theta synchronization.

Regressions. The regression model for average alpha desynchronization was significant ($R^2=0.708$, $R^2_{Adj}=0.635$, $St. Error=2.050$, $F_{Change}(1,4)=9.685$, $p=0.036$), as well as the coefficient ($B=0.128$, $St. Error=0.041$, $B_{Standardized}=0.841$, $t=3.112$, $p=0.036$). The regression model for frontal alpha desynchronization was significant ($R^2=0.742$, $R^2_{Adj}=0.677$, $St. Error=1.927$, $F_{Change}(1,4)=11.477$, $p=0.028$), as well as the coefficient ($B=0.159$, $St. Error=0.047$, $B_{Standardized}=0.861$, $t=3.388$, $p=0.028$). The regression model for right posterior alpha desynchronization was also significant ($R^2=0.747$, $R^2_{Adj}=0.683$, $St. Error=1.908$, $F_{Change}(1,4)=11.789$, $p=0.026$), as well as the coefficient ($B=0.115$, $St. Error=0.033$, $B_{Standardized}=0.864$, $t=3.433$, $p=0.026$).

Discussion – Study 3

Variation of the alpha rhythm was found to modulate 8-month-olds' correct responses on an age-appropriate VSTM task. When comparing mean power values recorded during Change Detection to those from a baseline resting-state, higher performing infants exhibited greater levels

of alpha desynchronization (lessening of alpha power during task-state) during cognitive activity, while lower performing infants exhibited greater levels of alpha synchronization (strengthening of alpha power during task-state). Previous studies have utilized a limited number of electrodes (Bell, 2002, 2012; Bell & Adams, 1999; Bell & Fox, 1992; Bell & Wolfe, 2007), which limits the close investigation of EEG activity in early development at high spatial and temporal resolution. However, Study 3 recorded high-density 128 channel EEG at a 500 Hz sampling rate, which allowed for more precise examination of infants' scalp topography. These results suggest that neural correlates of VSTM performance, as expressed via alpha desynchronization, may already be observed in infants by 8-months and may be readily indexed utilizing a combination of qEEG recordings and an age-appropriate oculomotor memory task.

Theta power was not found to modulate infants' Change Detection performance, implying that the developing alpha band may be more relevant for assessment of individual differences of VSTM abilities by 8-months-old. In this regard, decreases in alpha power during Change Detection may represent the brain's developing ability to inhibit distractors and focus attention (Bell, 2002; Bell & Wolfe, 2007; Libertus et al., 2009; Xie et al., 2018). To perform successfully on a given Change Detection trial infants must first encode the spatial locations and colors of three squares, retain them in memory over a delay, and then make a first fixation to the changed square as an indication of their successful memory for the changed square. Following the delay period, infants must inhibit the urge to look at distractor stimuli (squares that did not change color) and guide their oculomotor behavior to focus on the changed square. Similar to outcomes with older children and adults (Stipacek et al., 2003), Study 3 results express a linearly increasing desynchronization in infant alpha band power related to ascending Change Detection VSTM performance. Results also suggest that 8-month-olds assessed on Change Detection may perform successfully on three

square trials with delays up to 3000 ms, as no significant influence of delay duration was found on performance. Similar to Study 1, infants did not exhibit performance differences on Change Detection when assessed at the highest or lowest delay durations, providing additional evidence that infants' posterior parietal cortex, underlying Change Detection performance, may be robust to higher delays than previously tested by 8-months-old.

Study 3 results lend themselves to numerous avenues of future exploration, however, it is important to note the difficulty in making firm conclusions about the present results due to the limited sample size of infants tested. Therefore, it is recommended that future studies first perform replications with the Change Detection paradigm using a larger sample size of infants to confirm the results of Study 3. Once this relationship is verified through replication, future studies should examine whether the relationship between alpha desynchronization and VSTM is apparent when assessing infants with other age-appropriate VSTM tasks, such as Delayed Response and Delayed Match Retrieval. Such studies would ensure this relationship holds across unique memory tasks, and lend more evidence to alpha desynchronization as a promising neural correlate of early cognitive abilities.

Furthermore, future studies should longitudinally examine how developmental changes in alpha and theta power may predict performance on memory tasks at different ages throughout infancy. For example, the relationship of theta and alpha could be studied in younger infants, like 6-month-olds, to pinpoint the developmental time-course of when alpha activity may become more important than theta activity in relation to VSTM performance. For example, it may be possible that the associations found in Study 3 may not hold for 6-month-olds due to less frontal maturation at earlier points in development (Marshall et al., 2002), and that theta power may serve as a better predictor for younger infants due to immature development of regions associated with alpha.

Future studies should also examine how alpha desynchronization and theta synchronization may relate to infants' A-Not-B error performance. As shown in Study 2, infants' VSTM abilities were not found to be predictive of their B-trial performance, lending evidence to inhibition abilities possibly being responsible for successful A-Not-B performance. In such a study, if successful infants are shown to display higher levels of alpha desynchronization relative to their same-aged peers who display the error, this may add evidence to a further association between inhibition abilities being critical for successful A-Not-B performance, as well as provide another link between the relation of alpha power and inhibitory skills in early development.

Conclusions – Study 3

Study 3 provides new insights regarding links between early brain functions and fundamental memory abilities in infancy. Eight-month-olds' alpha desynchronization differentiated between higher and lower performing infants on the Change Detection VSTM task, but theta synchronization was apparently unrelated to VSTM performance. Study 3 also provides important tools for future research of infant memory abilities. For example, the distinct link between infants' alpha activity and their Change Detection performance may help shed light on development of different brain systems that subserve memory performance, in this case, the posterior parietal cortex. These results make a substantial contribution to the literature, by providing the first-ever multimodal assessment of the influence of infant alpha and theta activity on VSTM performance, demonstrating that (i) alpha desynchronization was representative of higher performers, (ii) alpha synchronization was representative of lower performers, and (iii) theta power was not informative in differentiating between higher and lower performers.

General Discussion

Results obtained from the integrative methodologies utilized in Studies 1-3 each provide answers to small pieces of a larger puzzle, that when taken together, begin to form a picture of how memory abilities develop in the human brain and how these processes are expressed on an oculomotor and neurological level in infancy.

Study 1 demonstrated that infant VSTM can be reliably indexed in 6–12-month-olds via two unique eye tracking tasks, Delayed Response and Change Detection. These tasks have been previously utilized independently as tools to index infant VSTM abilities, but it is important to note that Study 1 is the first to assess infants on these two tasks together in a task battery in order to compare relative performance within individual infants. The influence of delay duration was also examined, aiding understanding of how early VSTM durability is influenced by extended delays. Namely, higher delay durations were found to hinder performance for infants on Delayed Response, but not on Change Detection. This is important to highlight because previous infant studies have shown discrepancies amongst successful delays on with both Delayed Response and Change Detection (Brody, 1981; Oakes et al., 2013; Pelphrey et al., 2004). Furthermore, VSTM durability was more robust for Change Detection than for Delayed Response, adding evidence to the notion that frontal regions (important for Delayed Response performance; Diamond & Doar, 1989) mature at a slower rate than parietal regions (important for Change Detection performance; Tseng et al., 2012). Thus, Study 1 results imply the posterior parietal cortex is more functional in assessments of memory than the frontal lobe in 6-12-month-olds. Furthermore, Study 1 revealed that the Delayed Match Retrieval paradigm was not found to reliably index infants' VSTM, as this task may have been too difficult for infants up to 12-months-old.

Study 2 revealed that individual differences in infants' VSTM performance, as assessed via Delayed Response and Change Detection tasks, were not related to their oculomotor A-Not-B error performance. This is important to note, as the A-Not-B error has been considered to be an early developmental milestone representing maturation of memory ability (Cummings & Bjork, 1983a, 1983b). However, results from Study 2 revealed that failure on the critical B-trial may not be indicative of weak VSTM abilities, but instead, oculomotor errors may be caused by strong memories for previous hiding events at Location A which prevent infants with immature inhibitory control abilities from performing successfully on the B-trial (Diamond, 1990).

Study 3 uncovered associations between individual differences in neural alpha band power and performance on the Change Detection task. Specifically, higher performing infants exhibited lower levels of alpha power during Change Detection, while lower performing infants exhibited increases in alpha band power, relative to baseline. Previous infant studies have found relationships between neural activity and attentional abilities (Orekhova et al., 1999; Orekhova et al., 2001; Xiao, Shida-Tokeshi et al., 2018; Xie et al., 2018), however, Study 3 provides direct evidence that the developmental alpha rhythm may serve as a useful biomarker in evaluating functional development and maturation of the early cognitive VSTM abilities. Specifically, results suggest the alpha band may serve as a neural correlate of inhibition processes at play during VSTM tasks where infants must inhibit the urge to look at distracting stimuli.

Recently, the National Institute of Child Health Development (NICHD) has proposed a funding initiative involving measures of neurodevelopment. NICHD has made it a priority to fund comprehensive, efficient, low-cost measures of cognition in typically-developing infants that can be linked with developmental changes in brain structure and function, and that can be used for evaluating developmental status and intervention outcomes. Results of this dissertation may help

inform future investigators who seek to develop similar neurodevelopmental batteries for further investigation of memory and inhibition in typically or atypically developing infants. Specifically, age-appropriate eye tracking tasks such as Delayed Response, Change Detection, and A-Not-B, as shown in Studies 1-3, may be used in future neurodevelopmental batteries as indices of infant cognitive performance using delay periods up to 3000 ms. Furthermore, results of Study 3 suggest the alpha rhythm may provide a useful tool to track developmental changes in brain function relating to developmental status during infancy.

In conclusion, results of studies outlined in this dissertation provide new insight into the development of VSTM abilities in the human brain. These results increase the understanding of typically developing brain activity during the first year of post-natal life with implications for both basic and clinical research. These studies brought together a variety of physiological and behavioral measures that were informative in answering questions related to cognitive development when analyzed individually, as well as in combination. VSTM skills are known to be important for later memory abilities and further study of this phenomenon in detail during infancy will allow for identification of tools to aid researchers in evaluation of developmental status and interventions.

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